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GONADECTOMY

IN RELATION TO THE

SECONDARY SEXUAL CHARACTERS OF SOME DOMESTIC BIRDS

By H. D. GOODALE

Of the Massachusetts Agricultural Experiment Station

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CONTENTS.

	PAGE.
Introduction	5
The material	7
Juvenile characters	9
The operation	10
The anesthetic	10
Preliminary steps	11
Removal of testes	11
Removal of ovary	12
Description of cases	13
Ducks	13
Female ducks completely ovariotomized	14
Female ducks partially ovariotomized	17
Male ducks completely orchidotomized	18
Male ducks partially orchidotomized	20
Domestic fowl	21
Female fowl completely ovariotomized	21
Female fowl partially ovariotomized	25
Male fowl partially or completely orchidotomized	26
Age in relation to gonadectomy	31
The age of the feather germ in relation to the type of feather developed	31
Two types of females resulting from ovariotomy	34
Effects of gonadectomy on particular parts of the body	36
Effect on plumage	36
Effect on head furnishings	36
Effect on spurs	38
Effects on the voice and associated organs	39
Effect on the molt	39
Effect on color of the mandible	41
Effect on size	41
Effect on behavior	42
Effect on accessory organs of reproduction	42
Effect on the bursa Fabricii	43
Occurrence of characters of one sex in individuals of the opposite sex that are otherwise normal	43
Male characters in the otherwise normal female	43
Female characters in the otherwise normal male	45
Hen-feathered males	45
Inheritance of secondary sexual characters	46
Is the female bird a suppressed hermaphrodite?	47
The relation between breeding and gonadectomy	48
Darwin's and Wallace's theories of the origin of secondary sexual characters	49
Nature and mode of the ovarian secretion	49
Relation between the gonads and the secondary sexual characters in other groups	51
Summary	51
Literature cited	52

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GONADECTOMY IN RELATION TO THE SECONDARY SEXUAL CHARACTERS OF SOME DOMESTIC BIRDS.[1]

INTRODUCTION.

It has been long known that an intimate relation exists between the primary sexual organs of certain animals and their secondary sexual characters. Until recent years, however, there has been considerable doubt as to the interpretation of many of the effects of castration—*i. e.*, as to whether the effect tended toward the appearance of characters belonging to the opposite sex. In particular, there has been a dispute as to whether certain characters, such as the small comb of the capon, were to be considered juvenile or female. In birds the occurrence of individuals with the plumage and other characters of the male, but having the sexual organs of the female, have attracted a great deal of attention. Recently, Guthrie (1910) has described a hen with male plumage following ovariotomy, while Fitzsimons (1912) has reported like results in the ostrich.

Very often, and perhaps always, the records state that the ovaries of male-plumaged females occurring in nature have degenerated to a greater or less degree, and from this it has been inferred that the occurrence of the male plumage was in some way or other associated with the degeneration of the ovary. On the other hand, the sporadic occurrence of birds with the external characters of the female and the internal sexual organs of the male is relatively uncommon in races such as pheasants or domestic fowl. As a rule such males, whose primary sexual organs are perfectly normal, exhibit only one or two female characters, the remainder of their secondary sexual characters being those of the normal male. Female characters may also be normal to the juvenile male. Moreover, it has been shown in the case of hen-feathered males of the domestic fowl that this character is inherited in a definite fashion. The occurrence of male birds with the secondary sexual characters of the female, where these characters are distinct from those of the juvenile male, are extremely rare. It seems highly probable that, except in the very rarest of instances, female-feathered males are in an entirely different category from male-feathered females. (However, *cf.* Morgan, 1915.) Nevertheless, races exist, such as the bobolink, in which the males may become nearly or quite indistinguishable from the females at certain seasons of the year.

[1]This paper is based on work done at the Station for Experimental Evolution of the Carnegie Institution of Washington, while the author was a member of the staff at that station. It has been necessary, however, to include some observations made at the Massachusetts Agricultural Experiment Station, which relate either to matters of detail or confirm results previously obtained.

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Special attention is directed to those statements in the literature according to which the secondary sexual characters of the male bird do not develop after castration. Thus, Marshall writes:

"It is well known that caponization or the removal of the testes in fowl arrests the development of the comb and *spurs* and *other secondary male* characters which are normally present in the cock."[1]

As far as I can learn, the only characters for which the statement holds true are the comb and wattles, the crowing instinct, and the sexual reactions, and even here it appears that the last two are merely suppressed but not really absent, since both are occasionally observed in perfect capons. Certainly, whatever foundation there may be for such statements regarding the spurs and plumage is to be found in some other circumstances than castration. A further discussion of the point is given below.

It has not been easily possible to verify by experiment the inferences regarding the condition of the ovary in relation to the plumage and other secondary sexual characters, because its *complete* experimental destruction or removal has involved some practical difficulties, owing to its situation upon some of the main blood-vessels of the abdominal cavity. On the other hand, the experimental removal of the testes is accomplished with such ease that it has long been a common practice among poultry growers to castrate their surplus cockerels because of improved eating qualities. This result, however, may be secured without an absolutely complete removal of the testes and epididymis; that is, good capons are sometimes found with a small amount of tissue on the site of the testes.

The effects of castration on the secondary sexual characters of the cock have been studied by a number of observers, who report, in general, that, with the exception of head furnishings, the characters of the male develop in nearly the same way as those of the normal male. It is true that in some instances it has been recorded that these characters, such as spurs, luster, long feathers, etc., either fail to develop or develop imperfectly. However, anyone with a moderately wide acquaintance with poultry can easily observe many instances of the same sort among males that have not been castrated: Plumage which lacks in luster is common among males of low vitality, though otherwise normal; spurs develop very slowly in some races; the males of some breeds have relatively short sickle feathers, and so on. In other words, the characteristics described presumably have nothing to do with the results of castration.

True hermaphrodites may also exhibit characters of both sexes, but since they have the primary organs of both sexes present they can not well afford critical evidence on the points involved in this paper. The possibility that these may be genetically females will be discussed in the body of this paper.

[1]Italics mine.

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The terms primary, accessory, and secondary sexual characters have been used in their usual significance—*i. e.*, the primary organs are the testes in the male, the ovary in the female. The accessory characters are the vasa deferentia and the penis or papillæ in the male, the oviduct in the female. The secondary sexual characters include in a broad sense all the other characters in which the sexes differ. No attempt, however, has been made to cover so wide a field, but attention has been limited to the more obvious characters. There are many details of interest that thus far it has been impossible to study thoroughly and which will have to be left for the future.

In describing results, the words "male" and "female" have often been used in a purely descriptive sense. Thus, "male" feathers in a female means of course that such feathers are indistinguishable from similar feathers found in males, and so on. No implication is made as to the actual nature of the feathers.

THE MATERIAL.

During the course of the work, experiments have been performed on both pure-bred and cross-bred birds of both sexes, a majority of which have been pedigreed. The cross-bred ducks were derived originally from Rouen and Pekin crossed reciprocally. The cross-bred fowl were mostly from a White Plymouth Rock and Brown Leghorn cross. The results obtained from the cross-breds have agreed in a general way with those obtained from pure-bred birds. In detail, however, their use introduced some complications which are discussed in the body of the paper. For the pure breeds, Rouen ducks and Brown Leghorns were selected, not only because they represent the acme of sexual dimorphism among easily available domestic birds, but because they offered an opportunity to determine whether or not the male assumes female characteristics as a result of castration or whether the so-called female characters are in reality juvenile. Moreover, it seemed wise in the case of the fowl to have birds that were *relatively* homogeneous in respect to the size and form of comb, particularly for the work with the male. Previous observers of the effects of caponization, so far as I have had access to their papers, have not usually paid sufficient attention to the variety of fowl used. As it happens, the variety of birds used for capons, at least in this country, are mainly the small-combed breeds. Hence, at best, the capons would have relatively small combs. The Leghorns, however, have large combs in each sex, a feature which might affect the size of the capon's comb. Moreover, in heredity, the small comb is at least partially dominant over the large—*i. e.*, the offspring of a cross between a small-combed and a large-combed race approximated in size that of the small-combed parent.[1]

[1]Unpublished data.

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The plumage of the birds used in these experiments requires especial attention, partly because of the marked difference in the sexes, partly because of its complex nature and the succession of plumages during the life of each individual. At least two sets of patterns influence the general color of the bird. There is, first, the body pattern, which depends upon the arrangement of feathers of different form and color upon the body; superimposed on this body pattern are the patterns of the individual feathers. Any one follicle, however, may produce different kinds of feathers at different periods in the life of the bird. Thus all normal individuals, both ducks and fowl, experience a succession of plumage from the time they emerge from the egg to old age. What constitutes the adult plumage is a little difficult to say, for in some cases no plumage is quite like that which preceded it. In some varieties the difference between the plumage of the first and second winters is greater than that between the second and third. However, in both ducks and fowls the strictly juvenile plumages are quite distinct from the first mature plumage, so that for present purposes the plumage worn during the first winter by spring-hatched birds may be considered adult. In ducks there are three plumages: down, juvenile, and adult. In Brown Leghorns there are four: down, chick, juvenile, and adult. The distinctions between these plumages, as will be observed from the appended descriptions, are for the most part sharp and clean-cut at the height of development. Usually, however, because the plumage is changed piecemeal, two succeeding stages are intermingled. The descriptions are not intended to cover all details or all variations.

ROUEN DUCKS.

Down plumage.—Sexes indistinguishable; feathers in the form of down. Body: dull black dorsally; ventrally, yellow with a dark stripe through the eye and a similar one a little lower on the cheek and four dull yellow spots on the dorsal side of the body (plate VII, fig. *D*).

Juvenile[1] *plumage.*—Sexes similar but distinguishable; the down gives way to ordinary feathers; head stripes persist but the spots disappear; contour feathers dull black, with brown margins in the female. The male is similar, except that there are *no* brown margins on the feathers of the rump and dorsal surface of the wing; the rump feathers are greenish black; a few vermiculated feathers are present in various parts of the body.

Adult plumage.—Sexes quite unlike. Female (plate II):[2] head stripes persistent; entire plumage dull black and brown, the feathers sometimes penciled (plate VI, *o*), sometimes marked irregularly (plate VI, *m*,); no well-defined color areas. Male (plate I): no head stripes; several well-defined color areas, viz, green head, brownish purple breast, silver gray ventral regions, greenish black rump; remainder of dorsal surface dull black.[3]

BROWN LEGHORN FOWL.

Down plumage.—Sexes indistinguishable; mid-dorsal region rich reddish-brown edged with dark brown or black, becoming yellowish ventrally; a dark-brown stripe passing through the eye is separated from the top of the head by a buff stripe. Back with a longitudinal stripe on each side of buff and brown. Sometimes the buff stripe is nearly white, sometimes the brown is nearly black.

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[1]The word "juvenile" is used here for all plumage phases of the young and not in the limited sense used in the preceding section.

[2]In all the figures, due allowances must be made for the difficulties of reproducing the exact color values of the original specimen.

[3]The speculum, *i. e.*, iridescent blue bar of the wing, is alike in each sex.

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Chick plumage.—Sexes indistinguishable by color alone. Plumage as before, except that the remiges and rectrices develop precociously, together with a few feathers along the sides of the breast and belly. A few other spots also develop feathers precociously. The breast feathers are buff or brown; the rectrices and remiges buff and brown mingled irregularly. This plumage is perhaps a phase of the down plumage due to the precocious development of the main wing and tail feathers.

Juvenile plumage.—Sexes readily distinguishable. Female: buff breast, dull-black primaries, brown and black secondaries and tail feathers. Hackle laced with yellow, the center black and yellow mixed; remainder of the plumage brownish and dull black, closely intermingled as stippling. Male: Dorsal feathers short, but may be pointed at end in late stages; breast red and black or buff and black; rectrices black, primaries black, secondaries red and black; remainder of plumage red and black with some indications of the adult body-pattern.

Adult.—Sexes very different. The female similar in color to the female in juvenile plumage, except that as a rule the stippling is much finer (plate VI, *k*). The male has several well-marked body areas, viz, glossy black breast and belly, black wing front and bar (first and second row of secondary coverts). Feathers of the rest of wing and middle of back red with black centers, short but pointed. Saddle feathers long and pointed (plate VI, *l*), with black centers (sometimes absent in lateral feathers), and red or orange margins; tail coverts glossy black, long and curved, rectrices black. Hackles long and pointed, similar in color to saddle feathers. The red feathers of the back and wing and the saddle hangers are characterized by having a part of each barb modified into a bristle.

JUVENILE CHARACTERS.

The characters of the young are often spoken of as identical with those of the female. In many instances this is true, particularly for those characters of the adult male which are absent in the adult female, yet other characters appear only in the young, while a third set appears only in the young male; the last are sometimes specific, sometimes like those of the adult male. In the Leghorns there is no stage in which the young male, as a whole, is like an adult female, though he may be more like his mother than like his father in that both are brown. In the down, also, he is brownish (as well as his sister), but in an entirely different way from the adult female. The young drake in juvenile plumage on the whole resembles his mother far more than his father, just as the latter in the state of eclipse comes to resemble his mate. In the down his plumage, like the Leghorn's, is identical with that of his sister and neither are at all like their mother or father. On the whole very few juvenile characters in the young male are identical with those of the female. Even the young female has many characters peculiar to her age. In the young male Brown Leghorn the only character *almost* identical with a female character is the brown stippling on the feathers of the dorsal region in many individuals. His breast feathers are always red and black, never entirely buff. His comb grows faster than his sister's and is noticeably larger at a very early age, three weeks or less in robust individuals. The young drake has head stripes like his mother's, but this is about the only point on which there can be no question of the resemblance. His ventral feathers, while dull black with brown edging like his sister's, are not *penciled* like those of the adult female. On the other hand, his mandible begins to change color at a very early age. A few vermiculated feathers occur on parts of the body,

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while the feathers of his rump have no brown edging, as in both old and young females.

The exact nature of the juvenile characters must be taken into consideration when discussing the results of castration. The mere fact that a closer resemblance exists between the female and the young than between the male and the young can not be taken as an indication that the young are more female than male. The most obvious explanation of the resemblance is that the characters of both are protective and that natural selection has preserved them.

THE OPERATION.

The operation in each sex is very simple, the only difficulty being in the proximity of the great blood-vessels—the iliacs and the inferior vena cava—directly upon whose surfaces lie the organs of reproduction. In both males and females the preliminary steps are identical, except that for best results the male should be opened on each side. The female is opened on the left side only.

THE ANESTHETIC.

The anesthetic and method of administering it vary with the age and depend also upon whether the bird is a duck or chicken. Ether is the main dependence for most operations. This is given by inserting the head of the bird, or sometimes the beak only, into a bottle containing the anesthetic on cotton. Ducks have a trick of holding their breath the moment their head is inserted. They will inhale, however, the moment the bottle is withdrawn, so that by making false movements they may be induced to inhale the anesthetic. Aid may also be had by massaging the abdomen and chest. After a few inhalations have taken place the duck loses the power of inhibiting the respiration and begins to breathe regularly. With older ducks it is sometimes difficult to give enough ether readily in this way. Chloroform consequently is used for the first four or five breaths, just enough to overcome the duck's control of the inhibitory mechanism of respiration. More can not be used, for chloroform with both ducks and fowls is often quickly fatal. Very young birds are so susceptible to the influence of ether that it is difficult to keep them in exactly the right condition. By skillful manipulation, however, the bird may be kept in good working shape. With older birds the period during which the ether is given lengthens, while the intervals during which the ether is kept away become continually shorter until, with ducks 3 or 4 months old, it is necessary to give all the ether they will take after the abdominal cavity is opened; for as soon as this is done much less ether appears to be absorbed on account of the structure of the respiratory mechanism. It is usually advisable to have the bird thoroughly under an anesthetic before the opening is made, otherwise it is often impossible completely to narcotize the animal.

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In determining the degree of anesthesia, reliance is placed upon the amount of relaxation of the neck, the condition of the eyes—*i. e.*, whether open or closed—and the rate and depth of respiration. With good working anesthesia the neck is limp, the eyes closed, and the respiration deep and regular. Too much ether is shown by shallow, rapid, but often slightly irregular respiration. Too little is indicated by a rigid neck and often open eyes, though the bird gives few other indications of sensibility. Rapid respiration is often observed with too little ether.

PRELIMINARY STEPS.

The bird is fastened to the operating table by a cord around both wings, which are drawn over the back, while the legs are similarly fastened, but stretched at a medium tension in line with the long axis of the body. The feathers are plucked from an area extending from the fourth rib posteriorly over the thigh and from mid-line of the back to the center of the breast. An oblique incision is made through the skin from near the mid-dorsal line, slightly obliquely downward, following the anterior margin of the sartorius; then an incision is made between the last two ribs. This incision should be as large as necessary for convenience and will vary in different cases, care being taken to avoid extending the cut so far dorsally as to sever the spinal artery. The ribs are drawn apart by hooks and chain or suitable spreader.

REMOVAL OF TESTES.

In the male, except in very young individuals, the area of attachment of the testis is small, proportionally to the size of the organ. At the age at which the testes are commonly removed in commercial caponization the testes are ovoid in shape, while the vascular system is slightly developed. The connective tissue is also delicate, so that with modern instruments the removal of the gonads is a simple matter. In the adult the vascular supply has become well developed, the area of attachment absolutely larger, while the connective tissues are tough, necessitating the use of ligatures and knives in their removal. In the very young bird the testes are delicate; each has the form of a narrow cylinder, pointed at both ends, which is attached along one side to the iliac, rendering the removal correspondingly difficult. It may be readily accomplished, however, with a slender pair of curved forceps, but much care must be taken to avoid rupturing the iliac or the testicle. If the latter happens, it becomes very difficult to make a complete removal. The best procedure yet found in removing these very young testicles is to get one end started by picking carefully at the union with the iliac; the testicle can then be peeled off by keeping hold of the capsule on the iliac side with the forceps. Sometimes it may be found desirable, after the end has been started, to push off the testis with a wad of cotton. With older birds ordinary caponizing tools may be used.

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REMOVAL OF OVARY.

In the young female the ovary is a flat sheet of tissue, attached intimately by one surface to the ventral surface of the left iliac and vena cava. It may be removed in the following manner: Tear open the lateral peritoneum with tenaculum and forceps and also the dorsal peritoneum, which covers the ovary. Care should be taken to see that all loose ends are removed. The dorsal mesentery is then freed from its attachment near the iliac, extending from the anterior mesenteric artery posteriorly to a point somewhat posterior to the end of the ovary. This should leave the ovary and environs free from all membranes and the ovary ready for removal. With a pair of fine-pointed but blunt forceps the rear end is seized and gently pulled up. Sometimes there is a slight projection of the ovary rearward, which is free from the iliac. This greatly facilitates the starting of the ovary. If this projection is wanting it will be necessary to pick patiently at the end of the ovary and attempt to grasp it at its union with the iliac. Once the end is started, it is possible to proceed more rapidly. As soon as a sufficient amount is freed to furnish a secure grip, the end is taken firmly and a gentle pull anteriorly exerted, which slowly but surely peels the ovary from the iliac. It is possible to proceed in this way to a point near the posterior side of the adrenal. If one attempts to go farther forward, hemorrhage is pretty sure to result.

The next step is to attack the border lying over the adrenal. This is usually easily accomplished, since fear of injuring the adrenal need not stand in the way, though rupture of the adrenal vein is to be avoided, since the blood renders further proceedings less easy. The body of the ovary is freed from the adrenal around the anterior end and down the medial edge, peeling the ovary from its attachments toward the iliac. With the edges of the ovary freed on all sides, the anterior end is peeled back until less than a fourth of its length remains attached. From this point, one of two methods may be followed. The anterior end is seized with the forceps and the whole ovary stripped off, the line of tension being as nearly parallel to the surface of the iliac as possible; or, the forceps may be slipped beneath the ovary so that the anterior and posterior ends are doubled together and stripped off as before. If all has gone exactly right, there will be no hemorrhage, but a result as completely successful as this is rarely obtained; more often an apparently fatal hemorrhage ensues. If, however, a bit of cotton be laid upon the site of the ovary and the bird closed up as if all were well, the hemorrhage apparently ceases, for such birds rarely die, though they do so unless cotton is inserted. Autopsies after fatal operations show that the iliac has not been extensively ruptured, but that the wall has been made very thin or even broken through in places. The blood-pressure at this point is so low that the cotton is sufficient to prevent too great a loss of blood, while without the cotton the blood continues to flow.

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After the cotton has been inserted, all that is necessary is to close the ribs together with one or two ties, depending on the size of the bird. Finally, the skin is closed with a continuous suture. It is not necessary to remove suture or cotton at a later time, as they apparently never interfere with the health of the bird. It is not necessary to use any but the most ordinary aseptic methods.

DESCRIPTION OF CASES.

DUCKS.

During the course of the present work, females and males have been operated on, some with successful results, *i. e.*, complete gonadectomy; others with absolute failure, while many yielded partially successful

TABLE 1.—*Ovariotomized female ducks.*

Band No.	No. and character of operations.	Date.	Age at first operation.	Male characters first noted.	Results and remarks.
4	Uncertain.....	Mar. 11, 1909	11 mos...	July 4, 1910	Type II. Laying; egg in oviduct at operation; described in Biol. Bull., 1910; bird alive Dec. 1915.
	Examination..	Aug. 22, 1912			
20	Not certainly complete.	Aug. 19, 1912	4 mos...	Sept. 17	Transitory male characters.
24	Uncertain.....	Aug. — 1909	12 wks...	July 4, 1910	Type II. Described in Biol. Bull., 1910.
55	Complete.....	Aug. 20, 1912	77 dys...	Sept. 14	Type I approximately.
58	Complete.....	Aug. 20, 1912	77 dys...	Sept. 14	Type II.
62	Complete.....	Aug. 20, 1912	77 dys...	Sept. 14	Type II.
86	Two; both incomplete.	Aug. 17, 1912	About 63 dys.	.....	No male characters.
116	Complete?....	Aug. 7, 1912	11 to 12 wks.	Oct. 16	Type II. See text.
	Examination..	Sept. 7, 1912			
137	Incomplete....	June 13, 1912	About 10 wks.	Sept. 17	Transitory male characters.
	Incomplete....	July 30, 1912			
	Examination..	Oct. 16, 1912	.....	.....	Ovary found.
138	Incomplete....	June 13, 1912	.....	.....	No male characters.
140	Complete.....	Aug. 15, 1912	About 10 wks.	Sept. 4	Transitory male characters. See text.
	Incomplete....	Aug. 9, 1912			
	Uncertain.....	Oct. 16, 1912			
169	Incomplete....	July 31, 1912	45 dys...	Sept. 14	Type I.
	Examination..	Aug. 19, 1912	.....	.....	No ovary found.
173	Probably complete.	July 30, 1912	12 to 15 wks.	Sept. 4	Type I approximately.
	Examination..	Aug. 19, 1912	.....	.....	No ovary found.
174	Probably complete.	July 30, 1912	8 to 9 wks.	Sept. 5	Type I approximately. See text.
	Examination..	Aug. 17, 1912			
175	Two; no removal attempted.	July 31, 1912	.....	.....	No male plumage.
176	Complete.....	Aug. 9, 1912	.....	Sept. 4	Type II. Summer plumage unlike winter plumage.
177	Complete.....	Aug. 10, 1912	About 4½ mos.	Sept. 4	Probably Type I. Died Sept. 1912.
182	Complete.....	Oct. 31, 1912	4 wks....	.....	Type I. See text.

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results. These last throw considerable light on the process that results from the removal of the germ glands. Tables 1, 2, and 3 give a summarized history of those instances that yielded pertinent results. In addition to these, records are on hand of a considerable number of other successful experiments made at the Massachusetts Experiment Station. The detailed histories of several cases, selected as embodying the most important results of the work, are given in the text.

The terminology of the tables requires some explanation. The word "character" used in the heading of the second column refers to the nature of the operation—*i. e.*, whether the removal was complete, partial, or otherwise, as well as could be determined at the time. It does not refer to the actual result as determined by the later history of the individual in question. The date of the first appearance of male characters is almost always that of a feather character and depends, as stated below, upon the condition of the plumage at the time of the operation. In many instances feathers have been plucked in order that the change might be more readily observed. It is probable that the first visible change often occurs earlier than stated, but no attempt was made to examine the birds oftener than once a week. The number of operations on each bird can be inferred from the dates, when not specifically stated. The word "examination" means that the bird was opened to make an inspection of the site of the ovary. The word "approximately," used in connection with the Type I, means that the individual in question deviated slightly from this type through the presence of a few off-colored feathers.

Female Ducks Completely Ovariotomized.

No. 169. This bird developed as perfect a coat of male feathers as has appeared on a castrated duck, though others equally as good are now available. She is shown in plate III. Hatched June 16, she was a little over 6 weeks of age when operated on, July 31. A photograph taken a few days after the operation (plate VII, *D*, foreground) shows that the bird was still in the down and had not yet begun to develop the first coat of definitive feathers. Although the protocol states, among other things, that "removal was probably not quite complete," the results show that actually the removal was complete.

On August 19, a second operation was made, its object being an inspection of the site of the ovary. The protocol states:

> "A thorough and careful examination failed to show any trace of an ovary. However, to make assurance doubly sure, all the connective tissue on the site of the ovary was removed, except a little on the spot where the rent in the vena cava is apt to occur. As this could not be removed without danger to the vena cava, this spot was seared."

On September 5, it was noted that the juvenile plumage was like that of the young *female*, except the dorsal surface of the wings, some

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of the feathers of this region being male-like, *i. e.*, they lacked the brownish margin characteristic of the female.

On September 14 the first male characters, as indicated by the markings and color of the plumage, had begun to appear. Later in the year, when the juvenile to adult molt was completed, the bird had essentially the same appearance as that given in the plate. Since that time there has been no change in the character of the bird, though she has molted several times.

The bird, however, is not entirely a replica of a male. If the mandible be compared with that of the drake in plate I it will be observed that they are quite unlike. That of the male is typical for his sex, while that of No. 169 is typical for the castrated female and resembles that of the female. It differs from that of the normal female, plate II, in having the dark-greenish patches, mostly marginal, replaced by a clean yellow, or, to put the matter a little differently, the black area of the normal female was not affected by castration, but the dull greenish-yellow pigment did not develop. An explanation of this failure possibly lies in the age at which the black pigment becomes fixed. When first hatched, Rouen ducklings and many hybrids have bills that are almost black. In ducklings a month old the sexual differentiation of the mandible color toward that of the adult has already begun. In the male the colors gradually lighten until they reach the adult condition. In the normal females, however, very little apparent change takes place in the region where the blotch of the adult is located. The margins, however, gradually change to the color of the adult. A further discussion concerning this change will be found in a later section. It is possible, however, that something very different actually occurs. It may be that the black pigmentation of the mandible of the ducklings is a juvenile condition, and that in each sex this disappears, leaving an underlying condition which it has concealed.

No. 182. The history of this individual contains several features of particular interest. In the first place, the operation was performed when the bird was 4 weeks of age. She is one of the youngest ducks from which the ovary has been entirely removed. Hatched October 1, of non-pedigreed ancestry, the operation was performed October 31. Later developments show that the duck was of the "plain head" type described in an earlier paper. The juvenile coat (*i. e.*, first coat of definitive feathers) was not distinguishable from that of the normal female. Owing, perhaps, to the unfavorable conditions under which it was necessary to keep the duckling during her first winter, she grew very slowly and did not attain the adult plumage that winter. In March she again came under the immediate care of the writer and was given special attention. The more favorable conditions following on the long period of adverse environment apparently induced a molt, for

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the bird soon lost the juvenile coat and developed the adult coat of the male of this variety, which has a silver-gray breast (sometimes slightly tinged with purple) instead of the ruddy breast of the mallard, though the other secondary sexual characters are the same. The new coat of the duck was imperfect in many respects, but there was not the slightest doubt of its general character. No sooner had the feathers of this coat become fully mature than it was lost, being replaced by a coat like that of the summer coat of the male of this variety. That it was neither a juvenile nor female coat is shown by two things: First, a few feathers were vermiculated, a characteristic of the male's summer coat; second, this coat was replaced early in the autumn by the typical male plumage of this variety. In the summers of 1914 and 1915 the change to the summer plumage was followed by a return to the breeding plumage in the fall.

Besides being the first instance of the clear assumption of the summer plumage of the male by a castrated female, this bird is interesting in another point, *i. e.* she has never developed a good duck's voice. As already pointed out, only the female gives voice to the familiar sonorous quack. The drake never quacks, but produces a sound that can best be described as a *whispered* "qua." No. 182 has never been able to produce anything more than a broken quack, a sound best described as intermediate between that of the male and female, except when handled or otherwise subjected to special stimulus. Ordinarily she simply whispers "qua, qua," very much as the drake does.

In two respects, then, viz, assumption of summer plumage and imperfect voice, this individual approaches more closely to the male than any bird previously operated on. Both the site of the ovary and the corresponding region on the right side were examined in the autumn of 1915 by means of an operation. They were entirely empty.

Nos. 4 and 116. These two have been selected for description because they represent a different and important type of result following removal of the ovary. In addition, No. 4 is the oldest female from which an ovary has been successfully removed. As she has been described rather fully in an earlier paper, only a brief summary of the case will be given here. The first operation was made when the bird was nearly a year old. She was laying regularly immediately previous to the operation and in its course an egg with shell membranes fully formed was removed from the oviduct. The anterior half of the latter was also removed. By means of a second operation, August 22, 1912, it was ascertained that no trace of the ovary was present on the left side, nor as far as could be determined on the right, though a thorough examination of this side was impossible from the opening made on the left. The bird is alive at date of writing, December 3, 1915. The development of male characters has been very slight as compared to the cases just described. She is clearly in an intermediate condition,

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approaching more closely to the female than to the male in general color. However, since her feather coloring resembles neither the normal female nor the male in breeding plumage, it is perhaps better to consider this bird as a distinct type, designated below as Type II (plate IV). The majority of her individual feathers are either male or female in character and not a mixture of the two. The plumage as a whole, however, is a mixture, containing typical male and female feathers, plus a third type that is neither. The latter are brown and buff, but are barred transversely, either in a perfect or more or less broken pattern (plate VI, figs. *r* and *q*). On the ventral surface some feathers are more or less intermediate—*i. e.*, each feather shows both male and female characters. On the whole the condition approaches most nearly to that of the male in his summer plumage, but differs enough so that it can not be said that it is such a plumage, especially in this individual, which is very much more like an unaltered female than the bird figured. Further, this plumage is maintained throughout the year.

No. 116, a pure-bred Rouen, belongs to the same type as No. 4. Hatched May 18, 1912, the ovary was removed August 7, 1912, the removal being complete as far as an examination with the naked eye could determine. She was examined from time to time and no male feathers were found as late as September 7. Accordingly, the bird was opened and a careful examination made of the left side. No trace of any ovarian material could be found. The lack of male feathers a month after the operation was probably due to the fact that it was not ready to exchange the juvenile coat for the adult. Thus the feathers regenerating from follicles emptied at the time of operation belonged to the juvenile plumage. By October 26 the juvenile had been replaced by the adult plumage, which belonged to the type described for No. 4. The further history of the case is complicated by an attempt to engraft bits of ovary beneath the skin. Apparently, however, the implanted ovary was without influence, for feathers plucked at the time were replaced a month later by either typical male feathers or those of Type II. For a time the bird was not under observation, but in the spring of 1913 she had not changed in any essential. This condition was maintained throughout the summer, until the fall molt took place, when to my surprise she developed a much more perfect male coat, corresponding closely to that shown in plate IV, which is a figure of No. 24 described in an earlier paper. A discussion of this type will be taken up in a later section.

Female Ducks Partially Ovariotomized.

We may now turn our attention to some of the cases in which the removal of the ovary was almost but not quite complete. These cases throw considerable light on the effects of removal, besides giving us a more precise knowledge of the action of the ovarian secretion.

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No. 140. The first operation was made June 15, 1913. The exact age of the bird was unknown, as the original band had been lost, but she was approximately 3 months old. The ovary was apparently completely removed without hemorrhage. The apparently complete removal was demonstrated to members of the staff of the Station for Experimental Evolution at Cold Spring Harbor. Several weeks after the operation the bird had not developed any trace of male plumage. Accordingly, August 9, she was operated upon again. Lying over the suprarenal was a considerable mass of ovarian tissue, in addition to a minute piece farther back. Both pieces were removed. By September 7 new feathers had replaced those that were pulled at the time of the operation. The distal portions of the new feathers were female, the more proximal giving evidence of the absence of the influence of the ovary by transverse vermiculations, which, however, were brownish. By October 16 male feathers were present in various portions of the body. However, the younger feathers that were growing at this time were entirely female in character, indicating that some change had taken place. This led to a re-examination of the site of the ovary. This was empty, but attached to the mesenteries was a bit of ovary, the size of a small pea, while attached to the oblique septum on the left side was a bit of ovary containing one macroscopic ovum. Both were removed. However, no further progress was made in assuming male characters. The bird was kept until June 21,1913, when she was killed and examined. The oviduct was infantile, except that the walls of the vaginal region were somewhat thickened and corrugated. On the site of the ovary was a single small object like an immature ovum, about 1 mm. in diameter. On the right side was a body 5 or 6 mm. in diameter bearing (partially embedded) two small vesicles filled with a deep-yellow serous fluid. This body has not yet been examined histologically. Evidently, then, from the history of this bird we may conclude that a very small amount of ovarian tissue is sufficient to produce normal female characters. There is a point, however, at which, either because the amount of tissue is so small or possibly because of injury received during the operation, the fragment of ovary no longer suffices to produce female secondary sex characters. Similar results have been obtained in other cases, as, for example, Nos. 20 and 137.

Male Ducks Completely Orchidotomized.

The results of castration of drakes, as far as investigated, appear to be independent of age. Much, however, clearly depends on the completeness of the removal and, less clearly, on the nature of the material left behind. The testicles are not always readily removed, because in early stages they are cylindrical objects, pointed at each end and attached along one side to the iliac. In ducks, the elongated condition is maintained much longer than in fowl. In either case, if the correct procedure is followed, it is possible to remove the testicles com-

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pletely, even when in the elongated condition; though it frequently happens that, owing to the extremely fragile nature of the testes, they become broken. When this happens it is difficult to make sure that all testicular material is removed; that left behind is very apt to grow. A second difficulty arises because of the relation of the spermatogenic portion of the testes to the ducts. The Wolffian body lies upon the surface of the iliac and in intimate union with it. In removing the testes from young birds this is usually left behind, and in some instances it apparently develops independently of the spermatogenic portion. In a few instances birds have been subjected to autopsy without finding any trace of testicular material. Further work is required on this point, since, naturally, these facts have been learned as the work has progressed.

TABLE 2.—*Orchidotomized male ducks.*

Band No.	No. and character of operations.	Date.	Age at operation.	Results and remarks.
1	Left removed, right ligatured and left *in situ*.	Aug. 8, 1909	15 mos.....	Did not assume summer plumage in 1910, 1911, 1912, 1913, or 1914. In summer plumage when operated on. See text.
19	Right only removed.	Mar. 11, 1909	11 mos.....	Summer plumage in 1909.
470	Complete.....	Mar. 11, 1909	11 mos.....	Did not assume summer plumage in 1909 nor during the remainder of his life.
119	Left only.....	Aug. 9, 1912	11 to 12 wks..	Summer plumage. See text.
136	Left removed.....	June 13, 1912	About 10 wks.	Assumed summer plumage 1913. See text.
143	Both removed.....	Aug. 7, 1912	51 dys.....	No summer plumage. See text.
170	Complete.....	July 31, 1912	45 dys.....	No summer plumage.
171	Complete.....	July 31, 1912	45 dys.....	No summer plumage. See text.
172	Not certainly complete.	June 29, 1912	10 to 15 wks..	Summer plumage. See text.
186	Both removed.....	Oct. 31, 1912	4 wks.....	Did not assume summer plumage 1913. See text.

No. 1. This bird was over a year old when operated upon, August 8, 1909. He was in full summer plumage at the time. The left testis was removed. A ligature was placed tightly about the base of the right testis and this testis was allowed to remain. This bird did *not* assume the summer plumage in 1910, 1911, 1912, 1913, or 1914. He was killed in December 1914. No trace of testicular material could be found. Traces, however, of the vas deferens were found near its anterior end.

No. 171. This bird, a few days after the operation, is shown in plate VII, *D*, rear; hatched June 16, the testes were removed July 31, 1913. The protocol states that removal was complete but in fragments. The laterals and scapulars were just beginning to appear. The history of this bird was exactly that of a normal one to the time for the summer molt. June 10, 1913, the bird was molting, but the new feathers were exactly like the old, *i. e.*, the bird did not develop the summer plumage of the normal male.

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No. 186. The history of this bird is similar to the preceding. The testes were completely removed when the bird was 4 weeks of age. In 1913, 1914, and 1915 the bird molted but did not assume the summer plumage. At autopsy no trace of the testes could be found. It is of some interest to note that the molt took place at the same time of year in 1913 as that of No. 171, though No. 186 was 3½ months younger.

Male Ducks Partially Orchidotomized.

The history of the cases where the removal of the testes, intentionally or otherwise, was incomplete may be considered here in condensed form.

No. 119. August 9, 1912, the left testis was removed. June 10, 1913, the bird was found to be assuming the summer plumage. July 10, when the bird was in full summer plumage, he was killed. On the left was some testicular material. The vas deferens of this side was small and straight and scarcely visible. On the right was an immense testis, fully twice the size of that of a normal male. The vas deferens was convoluted and contained semen, but was not as large as usual. Penis and syrinx were normal.

No. 136. Left testis removed in several pieces, June 13, 1912. On July 1, 1913, the bird was killed while in full summer plumage. Vasa deferentia small, not easily seen. On the left was a small testis about a third the diameter of a normal testis, but of full length and irregular in shape. The right testis was normal, though a little irregular in shape.

No. 172. The testes were removed June 29, 1912. The epididymi were probably left behind, nor was it certain that all testicular material was entirely removed, though the sites of the testes were carefully wiped off. Whatever testicular material was left behind was not visible to the naked eye. June 10, 1913, the bird began to molt and to assume the summer plumage. August 10, when in full summer plumage, he was killed and dissected. On the site of each testis was a relatively small amount of testicular-like material containing numerous vesicles of approximately equal size filled with a yellowish fluid. The vasa deferentia were found with difficulty. They were very infantile and non-convoluted. The penis was rather small and contained only a little mucus.

It is perfectly evident that the male after castration often does not assume the summer plumage, but a number of points remain to be cleared up. While the sites of the testes have been found entirely empty in several instances where the summer plumage has not been assumed, there are also several cases where material has been found at autopsy on the site of the testes. While the histological examination of this material is not yet complete, it is probably not spermatogenic. On the other hand, where the males have assumed the summer plumage after castration, material that looks much like that just noted is always found. In several such instances, seminal tubules with spermatozoa

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have been found. It has seemed best, however, not to delay the rest of the paper to complete the histological work, especially as similar material has been found in castrated females (fowl)[1] and as a number of the birds are still under observation. It seems probable that the body found is the epididymis, which has developed in the absence of both germ cells and supporting cells.

DOMESTIC FOWL.

The operations on fowl yield results similar to those from ducks. The latter thus far have proved more suitable for experimentation because of greater hardiness and freedom from diseases, at least in the stocks available. Moreover, the ovary is removed more readily than from chicks. For these reasons fewer cases are available for the fowls than for ducks.

TABLE 3.—*Ovariotomized female fowl.*

Band No.	No. and character of operations.	Date.	Age at first operation.	Male characters first noted.	Results and remarks.
1193	.....	Mar. 31, 1911	4 wks.....	.....	Transitory male plumage. Described in Amer. Naturalist, 1913.
1196	.....	Mar. 31, 1911	4 wks.....	.....	Male plumage. Described in Amer. Naturalist, 1913. See text.
4042	Complete..... Examination..	Sept. 7, 1912 Dec. 14, 1912	.....	.....	Transitory.[2] Spurs developed well. Killed Oct. 10, 1913. Ovary regenerated.
4050	Incomplete.... Examination..	Sept. 6, 1912 Dec. 14, 1912	About 3 mos.	Sept. 19	Transitory.[2] Ovary regenerated.
4071	Complete.....	Sept. 6, 1912	About 3 mos.	Sept. 19	Transitory.[2]
4140	Incomplete.... Examination..	Sept. 6, 1912 Dec. 14, 1912	About 4 mos.	Sept. 22	New feathers completely male. Died Aug. 1, 1913. See text.
4154	Partial.....	Sept. 7, 1912	.....	Sept. 26	Transitory.[2] Oct. 12 ovary found.
4288	Complete.....	Sept. 4, 1912	32 dys.....	Sept. 26	Transitory.[2] Killed June 11, 1913.
4290	Complete.....	Sept. 1, 1912	32 dys.....	Sept. 21	Good male. See text.
4470	Possibly complete.	Nov. 13, 1912	66 dys.....	Nov. 26	Transitory.[2]
4471	Complete.....	Nov. 13, 1912	66 dys.....	Nov. 26	Good male. See text.

FEMALE FOWL COMPLETELY OVARIOTOMIZED.

No. 4471. Hatched September 8, 1912. According to the protocol made November 13, 1912, "a clean and complete removal of the ovary was effected." By November 26, male characters in the form of black feathers were visible in the breast. These continued to increase in

[1] *Cf.* Goodale, 1916. [2] Male plumage.

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numbers with the age of the bird until a complete juvenile plumage was developed, this being replaced in turn by an imperfect adult male coat. (It should be noted that in many *males* of the strain used, the full adult plumage, particularly in late-hatched individuals, may not appear until after the molt of the second season.) After the annual molt, the plumage had reached the adult condition. Plate v is from a painting of the bird made in 1913, when it was about 1½ years of age.

Certain points call for further comment. First, the plumage, particularly in proportion to the size of the bird, is more like that of the capon than that of the cock—*i. e.*, the feathers are longer. Second, the head is small and in the absence of a good-sized comb appears even smaller. Third, the bird as a whole is small, approximating the hen in size. Fourth, the shanks are comparatively short and of relatively delicate build, giving the bird a low-set appearance. Although the spurs are well developed, the legs are those of a hen and not those of the cock or capon.

The history of this bird during the summer of 1914 is of particular interest. It was observed that it molted in early summer and that the new coat was quite different from the old. The breast became suffused with red, because the new feathers were red and black, resembling strongly those of the young male. The dorsal regions lost their bright appearance and became relatively dull-colored. The individual feathers of the saddle were relatively short with rounded ends, and were stippled brownish red on a black ground. They were *not* colored like those of the female, though they had the shape of hen feathers. The distal portion of the feathers of the wing bow became black and red, instead of red alone, while the barbuleless margins disappeared. The secondary coverts became red and black instead of uniform black. These statements are sufficient to illustrate the character of the more important changes. By late August, however, the new feathers coming in were again completely normal male in character, and by early October the bird was well on its way toward the reassumption of the completely normal male plumage, which has been maintained ever since. It has been determined by an operation that no ovary was present, though an organ of an entirely different histological structure was found. (See page 24.)

No. 4290 is in many respects a parallel case to 4471, although somewhat older and castrated earlier in the year. Her history subsequent to castration and up to the time 4471 began to molt is the same. This bird underwent the usual molt, but showed only male feathers until killed late in November 1914.

As in the ducks, several instances have been observed where the assumption of male plumage was not complete, many of the feathers being in an intermediate condition, although the birds were completely castrated, as shown by autopsy or operation. One instance is

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No. 1196, whose history has already been briefly given in the American Naturalist, but which it may be well to give in more detail. The bird was purchased as a day-old chick from a breeder. The chicks of the lot of which this was a member were exceptionally strong and vigorous. This individual was first opened when 10 days old and a part of the ovary removed, but a hemorrhage started, so the operation was discontinued and the opening closed. Ten days later she was again opened and the remainder of the ovary removed with great ease and without hemorrhage. At the time of the second operation the chick was in the down except for the remiges and rectrices. The chick plumage (see page 9) began to come in soon after this. As this plumage is alike in the two sexes, no evidence of any results appeared until the juvenile plumage began to develop. From this time on, the bird exhibited the characters of the male except that the comb and wattles grew less rapidly than is the case in most normal males of this variety. At 6 months of age, while larger than those of the check pullets, these appendages were distinctly *female* in form and shape. Eventually they became equal in size and shape to those of many cocks. Unfortunately, the males that had been kept as checks on the rate of comb-growth disappeared, probably taken by rats; but even if they had not been lost, the comparison would have been of small value, since the normal variation in rate of comb-growth is so large. In due course of time the juvenile plumage was replaced by that of the adult male, though differing in two points: first, the sickles of the tail were missing; secondly, many of the feathers of the saddle region were not long, pointed, and golden-laced with black stripes, but were broad, rounded at the ends, and colored dark brown with minute red spots or stippling (fig. c, American Naturalist, 1913). In shape and size they were identical with those of the hen, but the coloring differed, being more like similar feathers found in this region in the juvenile plumage of the male. The bird was kept until she was well into the molt of the second year, in hopes that these would be replaced by typical male saddle feathers. Nothing of the sort happened. Each kind of feather was replaced by one of the same kind. In other words, no further development of the plumage toward the male type occurred. In the light of other observations, it is probable that even if the bird had not been killed at this time she would not have developed more of the male plumage.

The non-development of the sickle feathers of the tail may be explained in the following manner: The dorsal part of the uropygium was missing, resulting in a deficiency in the number of rectrices, there being only 8 instead of the usual 12 or 14. The oil gland also was missing. Moreover, a rumpless cock appeared in a younger brood obtained from the same breeder. Correspondence brought the fact that such birds occasionally appeared in his home flock. The evidence, then, indicates that the deficiency in sickles and tail feathers had nothing

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whatsoever to do with the absence of the ovary, but was purely a coincidence.

The findings at autopsy, illustrated by fig. *C*, plate VII, are of particular interest. On the site of each germ gland was a mass of whitish tissue, and leading from it to the cloaca was a slightly convoluted tubule. On the left was a distinct but infantile oviduct. No trace of one could be found on the right. On the right "gonad" were several vesicles filled with a rather thick but clear yellow fluid. Sections of these "gonads" showed a compact mass of small cells having a large nucleus in proportion to the protoplasm. The whole mass suggested nothing so much as early nephrogenous tissue. There was not the slightest trace of seminal tubules nor of spermatozoa, nor was there any trace of degeneration. According to Foges and others, transplanted testicular tissue always contains seminal tubules and spermatozoa. It seems probable, then, that after the removal of the ovary the Wolffian body and ducts underwent a compensatory development. It is well known, of course, that the right ovary degenerates in female birds and that in the male the Müllerian ducts disappear; but, according to Lillie, nothing is known of the fate of the Wolffian ducts in the female.

The hermaphroditic condition of the accessory organs of reproduction in this individual led to a search for similar organs in normal females. In some individuals it is comparatively easy to demonstrate on the right side a small amount of tissue that may be interpreted either as the degenerated gonad or the remnants of the Wolffian body of this side. Leading from this is a strand of tissue which can be interpreted as the Wolffian duct. In most females it is impossible to demonstrate these traces, but several young normal females have been found in which there can be no doubt of the existence of these structures. Whether or not they are really the rudiments of the Wolffian body and ducts remains to be determined. On the left it is almost impossible to find traces of the "Wolffian body," but the "duct" can sometimes be found. A further investigation of these structures is being made in the hope that their nature may be definitely determined.

If the observations of Beard and Allen regarding the original source of the germ cells in the endoderm are correct, and if Ancel and Bouin are correct in referring the production of the internal secretion of the testes to the interstitial cells, the degree of comb development may be referred to them rather than the germ cells. To determine this point involves considerable histological work which as yet it has been impossible to accomplish. In the present instance we have had a large comb develop on a bird in the absence of the germ cells proper. Of course, it is possible that some of the cells of the glandular mass may have been potential germ cells, but there is no evidence that such is the case. On the other hand, the large comb and wattles developed

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slowly, probably accompanied by the development of the "Wolffian body" *pari passu*. A further discussion can best await the results of the examination of several other instances of similar nature now on hand.

No. 2058. This bird is of considerable interest. She is a pure-bred Brown Leghorn from the stock of one of the best-known breeders of the variety in this country. She was 2 months of age when the ovary was removed. In 2 weeks the first male feathers had begun to appear. The development of male characters continued until late in the fall, when she was a very good young male in appearance. As stated above, young males and castrated females under some circumstances are slow in reaching a complete development of the adult plumage.

In this instance, the bright feathers of the wing bow were relatively few in number, while the hackle, back, and saddle feathers, though of adult color and shape, were quite short. While she was confined during the winter, most of the saddle feathers were picked off by her mates. The new feathers that came in were short, rounded at the end, and without barbuleless barbs; the ground color was black, the distal portion of the shaft often red, and the web sometimes sprinkled with minute brown spots. As somewhat similar feathers may often be seen in young males, little attention was paid to the matter until late in the summer of 1914, when it was observed that the bird was not developing the expected adult male coat of feathers. The shape and size of the feathers of the new coat are more like those of a hen-feathered male, while the color of the feathers of the back, saddle, and wing bow remained essentially as described. The rest of the bird is colored like a male. This bird has a well-developed comb, wattles, and spurs, and in a sense corresponds to the Type II of the ducks. By means of an operation it has been determined that no ovary was present.

Female Fowl Partially Ovariotomized.

In several instances the ovary has not been entirely removed; indeed, in some instances, only a small fraction was taken out. In such cases no changes followed the operation. From other individuals almost all the ovary was removed, so much so that male plumage was developed in varying degrees, though no definite relation between the amount of ovary removed and the degree to which the secondary sexual characters of the male developed has been made out, because the exact amount of ovary left has not been known, though in a few instances none could be seen with the naked eye.

An interesting example of incomplete removal is afforded by No. 4140. This individual was a hybrid female, whose original band had become lost. She was about 3 months old at time of operation and had well-developed female plumage. The removal, according to the protocol, was probably complete, though it was possible that a little

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remained, since the posterior portion did not come off as neatly as could be desired. A slow hemorrhage, however, permitted a rather careful examination of the site of the ovary, and this showed no trace of ovary. September 22, male feathers had begun to appear, but after a time female characters appeared on the younger portions of the feathers and, of course, those feathers that developed after this were altogether female. December 14 an examination was made. At the extreme anterior end of the original site of the ovary was a piece the size of a pin-head with a few ova just visible to the naked eye. These ova were destroyed. Near the center of the site were 3 ova, each 3 or 4 mm. in diameter, which were left in place. Careful scrutiny failed to show others. No ovary was visible on the right side of the bird. August 1, 1913, after an illness of several weeks, she died in an emaciated condition. The right side was completely empty. On the left, in the same situation as the 3 ova mentioned above, which had in the meantime disappeared, was a little tissue that gave no indication of being ovarian. The oviduct was infantile. At death the plumage was a mixture of male and female feathers, but the numerous new feathers that were coming in were all male. In this individual there was first a partial assumption of male characters, followed by a change to female characters and finally again to male characters. These changes paralleled the removal of all but a minute portion of the ovary followed by a partial regeneration, which in turn was either removed or degenerated.

Other instances with a similar history might be described. In some only a few feathers developed male characters partially or wholly (plate VII, fig. *F*); others developed more. In two instances, which were pure-bred Leghorns of the same stock as No. 2058, each developed a complete juvenile male plumage by early fall. Both lost the feathers from the back by the feather-eating habits of their companions, and in each instance the new feathers that came in were female in character. In June, both birds were opened and in each considerable ovarian tissue was found and as much of this as possible was removed. Three weeks later, the appearance of male feathers had begun in both birds, but stopped soon after. Later, one of the two resumed the development of male characters. In several others the spurs continued to develop, although the plumage reverted. The relation of spurs to the ovary will be discussed later (page 38).

Male Fowl Partially or Completely Orchidotomized.

The removal of the testes has been a common practice, commercially, for centuries, in order to increase the size of the bird and also to improve its flavor. It seems probable, however, that what really happens is that while the size is increased, the flesh is not improved, but remains in the condition of the young bird much longer than it

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would otherwise. Whatever improvement, if any, in flavor is due more to special methods of fattening than to removal of the germ glands. In the absence of the latter, the capon retains certain of his youthful characters much longer than he would otherwise, but it is very doubtful whether a young cockerel fed and cooked the same as a capon could be distinguished by taste alone from the latter. Coinciding with the time of sexual maturity, the cockerel of the market breeds become "staggy," a condition characterized by a hardening of the muscles with the development of a greater amount of connective tissue. The commercial advantages of caponizing are found in greater size and slow maturity, with accompanying retention of the soft, richly flavored flesh. Eventually, however, capons become hard in flesh.

The capon has been investigated, as a matter of scientific interest, by several students—Foges, Halban, and others. They reach essentially the same results, though there are some contradictions which, however, are easily explained. They are agreed that while the comb and wattles remain small, the plumage is essentially like that of the male, except that it lacks brilliancy. However, normal males often lack a good color, due to late hatching, overcrowding, poor growth, and other unfavorable conditions. Indeed, the plumage of capons when properly cared for is fully as brilliant as that of normal males. None of these observers states the variety of fowls used, an important feature, as the males of some breeds have very small combs and wattles. The spurs, too, vary much in the age at which they appear. In Leghorns spurs 10 mm. long have been recorded at 3 months of age. In some Plymouth Rocks and Brahmas they are just beginning to appear when the birds are a year old. If this variability among normal males be given due consideration, the discrepancies in the observations may be accounted for.

For the present study, the Leghorns were selected, among other reasons, because, first, they are not commonly caponized; second, in each sex the comb and wattles are very large; third, the spurs appear in the males at a comparatively early age. In a breed with these characteristics we find the following histories after castration:

Seven pure-bred Brown Leghorns were castrated when from 21 to 28 days of age, although commercially males are caponized at 2 to 3 months of age. At this time they possessed, in addition to the down, only remiges and rectrices. Two of the birds were kept until they were 16 months of age, while the other two were kept until 4½ years of age. One of the two that was killed at 16 months had long been recognized as different from the others. He was more active and inclined to pay attention to the hens and grew a relatively large comb and wattles by the time he was 6 months of age. However, he was never observed to crow, though often watched and though particular efforts were made to get him to crow. On making the autopsy, a piece of testicle con-

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taining spermatozoa was found attached to the abdominal wall. The *sites* of the testes were empty. The other bird, externally, was characteristically a capon and did not differ from his mates. At death no trace of testicular material could be found. In all four the normal male plumage had developed, except that the feathers were longer. The spurs, too, were well developed. The comb and wattles, however, remained small, though of course not of the size they were when the operation was performed. The two kept for over 4 years have interesting histories. When 18 months old their combs began to grow rather rapidly and continued to grow for several months before ceasing. During the winter of 1913–14 the combs began to grow again, but, unfortunately, during the severe weather lost the points through freezing. On this account the final size can not be accurately determined, but it is obvious that they reached nearly if not quite their normal size.

Further experience with capons shows that the comb development of the bird figured by Goodale (1913, American Naturalist) is greater than that which occurs in other instances, such as that shown in plate VII, *A*, which has almost no comb development. True, the comb is not as small as when the bird was castrated, but the enlargement is only that necessary to correspond to the increased head size. It is now evident that the comb of the bird figured in the Naturalist paper had already begun to grow at that time, although for a bird 16 months of age the comb shown in the figure is much smaller than that of the normal hen, to say nothing of the cock. At that time it was supposed that the amount of comb tissue present was due to the genetic basis in the Leghorns for a large comb. This assumption is supported by the absence of testicular tissue in a mate with a similar history which was autopsied and by the relatively rapid growth of the head furnishings in another mate, which at autopsy had a small bit of testicle containing spermatozoa, attached to the abdominal wall, although it lacked other testicular material. The capon figured in the Naturalist was killed October 17, 1915, when somewhat more than 4½ years of age. The bird weighed 5¼ pounds and was very fat, resembling in that respect an old hen of the American breeds. On either side was a mass of testicular-like material; that on the right was 18 mm. long by 10 mm. in diameter, that on the left 12 mm. by 6 mm. Leading from each was a small but distinct vas deferens. No spermatozoa could be identified, either in the vas deferens or in the organ itself. Nor was there any evidence of sperm formation. The bird was in good health and had been running with hens for a long time. As far as could be made out, the "organs" were in good condition.

Although both birds had combs of similar size at the time the photograph mentioned above was made, eventually one (No. 1177) outstripped the other, developing a comb that was only a little smaller than that of a normal male. At the autopsy of No. 1177, which died on

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July 16, 1915, in addition to organs similar to those of No. 1192, a piece of tissue, 3 by 5 mm., was found attached to the mesentery, which on sectioning proved to contain no spermatozoa or seminal tubules. On the contrary, its structure was very similar to that of the same material found in No. 1192. The possibility that this tissue is really spermatogenic, but degenerate because of its age and its position on the mesentery, can not at present be excluded, owing to the lack of sufficient comparative material, particularly testes from normal old cocks. Testes, however, from one old drake and one old cock have been examined and found to be normal. The early history of No. 1177 is similar to that of No. 1192, but his later history differs slightly in that his head furnishings grew to a larger size than those of No. 1192. He also became more active and had much the bearing of the normal cock.

In early maturity these two capons were not kept with hens, but with cockerels. During the winter of 1912–13 they ran with hens along with normal males. In March the normal males were removed; shortly after, the capons were observed treading the hens. They were never seen chasing the hens, but when hens squatted on their approach the capons mounted them and completed the sexual reaction. There was no evidence of desire on the part of the capon, but his reactions to the sight of the receptive hen indicate the existence of an instinctive complex motor response to the specific visual stimulus.

The mating reaction between normals strengthens the interpretation given of the capon's behavior. The psychological condition of each of the principal actors is an important factor in determining the course of the mating process. As a rule, the male is always ready to copulate. The hens, however, vary. Some seem always ready, others never ready, while others vary from time to time. If a hen is ready for copulation she will squat and hold out her wings ready for the male to mount whenever he approaches. Under such circumstances he will mount the hen and complete the sexual act, even though as far as one can see such intention was far from his mind. In other words, the action of the hen starts a complex reflex. Such is what happens when a mating occurs between the capon and hen; but in matings between normals it often happens that the hen is not ready when the male approaches, and if he attempts service she avoids him. If he is particularly anxious for service he may chase her and eventually force service. This sort of mating has not been observed on the part of the capons. Their matings, on the other hand, so far as observed, have always been in response to the female's solicitation.

For surety's sake, a large number of the eggs of these hens were examined, but all were found to be infertile. Later in the season, on two or three occasions, the capons were seen crowing. The crow was to all intents exactly the crow of a normal cock. This is inter-

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esting, as it is unlikely that the birds had ever crowed before. The reaction was shown for only a brief period, under very favorable weather conditions in the spring. The males were kept with the females throughout the summer, but were not heard to crow again that season, although under daily observation. The mating reflex, however, was also kept up.

During the summers of 1914 and 1915 these capons were again allowed to run with a large flock of females with which no other males were kept. The behavior of these birds has been very much like that of a normal male. I have not seen them chase the hens, but have seen them tread the hens under the same circumstances as before. Both crew occasionally and No. 1177 crew a good deal. He had a larger comb than the other, was more active, and carried himself in the erect, tense posture of active males and seemed more willing to tread the hens. The pugnacity of both was tested by introducing a strange male from time to time. On one or two occasions a fight resulted, in one of which the more active capon (No. 1177) came off victorious for the time being. After a few hours, however, the normal male returned to the attack and drove both the capons off the floor. It is possible that the temporary victory of the capon was due to the somewhat dazed condition of the male when placed in the pen. As a rule, these capons have either left the field at the first onslaught or fought very briefly. Usually, they did not make the first attack.

The autopsies on these birds show that while they were undoubtedly almost completely caponized, there was a regeneration of tissue, the exact nature of which will be reported upon later. It seems evident, however, that this regeneration must have been slow and that to it must be referred the growth of comb and wattles after a year and a half.

Of another set of 4 Brown Leghorns castrated August 5, 1913, 3 proved to be good capons. They were kept with hens, males, and other capons during most of the year. Two were used to brood chicks in 1914. One of these was seen crowing in September of that year. He was also noticed circling the hens, but as far as observed did not tread any.

A number of Rhode Island Red and Silver Penciled Wyandotte capons also were under observation, and these, too, were essentially similar both in respect to appearance and behavior. Several of these were examined and found to be completely caponized; in others, however, small amounts of tissue, like that noted above, were found.

The results of removal of the testes from the young cockerel may be stated as follows: His plumage at a suitable age becomes identical with that of the cock, except that his feathers are longer. The comb and wattles do not develop, except in proportion to the increase in skull size. The spurs are like those of the cock, but become pointed at an age when the latter's are still blunt. His behavior is anomalous in

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that, though usually quiet and voiceless, he sometimes crows, sometimes shows the male sexual reaction, and may brood chicks. (Plate VII, fig. *G*.)

There is another peculiarity of the capon that I have never seen described, although it seems impossible that it could have escaped notice. The first row of coverts covering the primaries become disproportionately long, while the secondary coverts retain their normal proportions. The disproportion is shown in plate VII, *E*. This increased size of the primary coverts is of considerable importance, since it indicates that the feathers differ in their response to the secretions of the testes. While, as stated above, the feathers of the capon in general are longer than those of the cock, the coverts grow much longer than any of the neighboring feathers.

AGE IN RELATION TO GONADECTOMY.

The age at which the operation is performed may influence the final results in one of two ways: First, the character, such as a mature feather, may have ceased growing and therefore be non-modifiable. Secondly, it may be still growing, or it may resume its growth subsequent to the operation, so that in either case there is the possibility of modification. Moreover, age might influence the type of modification through its action on other parts of the body. That is, a bird castrated when 3 weeks old might give an entirely different result from one castrated at 3 months, but thus far, aside from structures which are no longer growing and therefore no longer subject to the influence of the gonad, no constant relation to age has been observed.

Since, however, the young bird is less differentiated than the older, greater changes would be expected. If it were possible to destroy the germ glands at the proper time during the embryonic life, the female embryo possibly might become transformed somatically into a male.

AGE OF THE FEATHER GERM IN RELATION TO THE TYPE OF FEATHER DEVELOPED.

It has happened in a number of instances that the female bird has been molting at the time of the operation. Individual feathers from such birds often show both male and female colors, color patterns, and even shapes, the area occupied by each depending upon the age of the feather germs; the younger the feather the larger the area of male characters. The colors are often separated by a clear-cut transverse line in both ducks and chickens. The effect is more striking in feathers from fowls than in those from ducks, largely because of the kind of characters involved. The cleanest-cut instances have been observed in Brown Leghorn pullets, particularly in the breast feathers, which are salmon-colored in the normal female but black in the male. The modified feathers are salmon-colored at the distal end, but at some

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more proximal point change abruptly to black. The position of the line separating the two colors varies with the age of the feather germ at the time of the operation, those feathers which have the greatest amount of black (*i. e.*, which have the line nearer the tip) having been the youngest when the ovary was removed. The line of demarcation is sharp, showing that the secretion of ovary does not persist in the circulation for any considerable length of time after the ovary has been removed. A series of such feathers is shown in plate VI, *a* to *g*.

Many of the combinations theoretically possible have been observed. The distal end of the sickles may be stippled brown and black (female), the proximal end a uniform glossy black (male), or *vice versa*, the latter occurring where the ovary regenerated. Saddle feathers may be observed with male tips and female bases (plate VI, *i*); others may have partially female tips and male bases (plate VI, *s*); while a third group has been seen with female tips, male intermediate portions, and female bases (plate VI, *h*). In these instances, while the male end, for example, is colored like that of the female, its shape may be more like that of the female, or *vice versa*. Indeed, some of the expected combinations, while realized in point of color, are not realized in point of shape, size, and arrangement of barbules. Thus the tip, while rounded, may be narrower than in the case of purely female feathers. This lack of expected combinations may be due to the amount of differentiation already undergone by the cells of the feather germ at the time of the operation. That is, the cells for the feathers may already be cut off, but there are not enough to produce a full-sized male feather. Or, the large outlines of the feather may be already laid down, and hence unchangeable, while the color has not yet been determined. The observed combinations are undoubtedly due to the mechanical and time relations in the development of the various parts of the feather. Thus, it is not very likely that any feather will have a very broad, rounded, and stippled tip, followed by a narrow black portion with golden margin, as such feathers are too short to permit a change of this character. That is, it is probable that if the distal end of the feather has been laid down so as to produce a typical female feather, a considerable change in the basal end will have been rendered impossible.

When the removal of the ovary has been so incomplete that male characters develop in the plumage for a time only and then cease, feathers male at the distal end but female at the proximal end may be observed. For example, instead of a buff tip and slate base, which is normal for female feathers, there may be a black tip followed by only the slate-colored base. Since the under-color (proximal half) of the normal female breast feathers is slate and merges gradually with the salmon tip, the line of separation is not as clear as in the reverse case. Similarly, the tip of the saddle feathers may be male, the base female (plate VI, *i*). In one case, the tip of the saddle feathers were female for

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several millimeters, together with the center and most of the base, but along the edges of the tip, for about 6 mm., the feathers were distinctly male, the barbules being absent and the barbs orange in color.

Like results have been obtained in several instances with the ducks, but in only one is the interpretation free from complications, due to the close resemblance of the female's plumage with both the juvenile and summer plumages of the male and partly to the type of plumage found in the females of Type II. There is no question, of course, as to the nature of the male portion of the feather, provided it belongs to the breeding plumage. Whatever questions may arise are in regard to the female portion. Plate VI, *p*, shows one of these feathers. Doubtless more instances would have come under observation if particular pains had been taken to select birds in the right stage of development when operated on.

Feathers that even for a small portion are male along the margin but female in the center, or *vice versa*, do not fit well with the suggestion that the ovarian secretion does not persist long in the circulation. However, another sort of explanation may perhaps be offered for such cases, and that is that some of these characters are more responsive to slight amounts of the ovarian secretion than others. From the evidence presented above, it is quite certain that, although a minute particle of the ovary may be present, the amount of secretion produced may be insufficient to bring about the development of the female characters. As this particle grows the amount of secretion produced must constantly increase until it reaches a point where the male characters are completely suppressed. In between these may be a region where the amount of secretion present in the blood is sufficient to suppress some male characters, but not all.

A different explanation may be offered to account for those instances where the color distribution in a transverse line is both male and female, but where this condition covers a very small portion of the feather and then gives way to a purely male or female condition, as the case may be, since obviously the relation of the barbs to the axis while in the sheath is sufficient to account for the final relationship of the characters.

The whole matter is further complicated by considerable variation in the characters in question, in some portions of the plumage at least.

It may be possible to utilize this sort of data in studying the order in which the various parts of the feather are laid down. Thus, those feathers that have the margin on any transverse line of one color and the center of another color indicate that the corresponding parts in the feather germ are differentiated at different times, the margin being formed later than the center. On the other hand, from those feathers in which the transverse boundary line between the two colors is very sharp, one could conclude that the differentiation extends in a well-defined line transversely to the main axis of the feather cylinder.

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TWO TYPES OF FEMALES RESULTING FROM OVARIOTOMY.

In the course of the work it has been necessary to use both pure-bred and cross-bred female birds. Curiously, in the case of the ducks, the cross-breds after the operation have developed a more perfect resemblance to the male's plumage than the pure-bred. Not one of the latter (five in number)[1] has produced a bird that did more than develop male plumage to a certain degree, while the plumage of the least perfect of the cross-breds approximates that of the male more closely than the most perfect of the pure-breds. The results with the pure-breds are not due to imperfect castration, for this type of plumage is maintained for years, in one instance for nearly 6 years. Moreover, at autopsy the birds have been found free of any ovarian tissue. During the second winter the plumage is frequently more male-like than during the first winter. Two of the pullets also failed to develop a perfect coat of male feathers, though they were the ones that developed the comb and wattles

TABLE 4.—*Comparison of the two types of female ducks resulting from ovariotomy.*

	Type I.	Type II.
Head	Drake	Some green feathers, especially dorsally. Remainder female-like.
Neck ring	Present	Present.
Breast	Drake	Mixed brown and buffs, but not arranged in the female pattern. Feathers of this type are shown in plate VI figs. *r* and *q*.
Belly	Drake	Mixed drake and duck.
Shoulders	Drake	Mixed drake and duck.
Back	Drake	Drake.
Wings	Drake	Drake.
Rump	Drake	Drake.
Tail feathers	Curled	Curled.
Bill	Black and yellow	Black and yellow.
Voice	Duck	Duck.

which most perfectly resembled those of the male. They also were pure-bred. Many of the cross-bred ducks, however, failed to develop into quite as good replicas of the male as No. 169. A few feathers in certain parts of the body retain a resemblance to the female, so that on the whole the demarcation between the two groups is not altogether clear-cut, though there is little difficulty in placing an individual in the proper class. The difference between the two types is shown in table 4. The word "drake" or "duck" is used to indicate that the character in question is like that of the male or female respectively.

If we survey the cases in which the male plumage is the more imperfectly developed, it appears that those regions which in the males become most like the females during the summer molt are the same regions that, in the castrated females, tend most strongly to retain female characters. These regions are the head and ventral surface, especially

[1]Two non-pedigreed females, probably but not certainly pure-bred, castrated in 1914, belong to this class.

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the breast and belly. In the belly region the markings of the feathers in both the castrated female and the male in summer plumage are vague, but usually show a certain amount of vermiculation. The feathers of the breast regions in each of the three plumages (breeding male, summer male, and female), however, have a distinct pattern, which is often very varied and exceedingly difficult to describe briefly. In the female, the feathers are brown, penciled concentrically with buff or else more or less spotted (*cf.* plate VI, figs. *m* and *o*). In the male they are self-colored claret. In the summer plumage of the male they are again distinct, having a reddish tip, the remainder being buff and brown, but with at least one or two transverse bars (*cf.* plate VI, figs. *r* and *q*). In the castrated female the feathers of this region approach most closely to the latter type. The transverse buff or reddish-buff bars are characteristic of the summer plumage of the male and of Type II females. Certainly they bear no resemblance to the plumage of either the breeding male or female. In the head region of the castrated females a mosaic is usually formed, part of the feathers being distinctly male, the other of a nondescript semi-female character. The remainder of the dorsal region is always approximately male, except for some of the scapulars.

Why so many of the castrated females should develop a plumage that in part is very much like the summer plumage of the male is not at all clear. It can not be due to the absence of all gonads, as recorded above, for in the male the absence of such gonads results in a failure of the male to assume the summer plumage. Moreover, this plumage is not characteristic of all castrated females, since some develop the entire male breeding plumage. It would seem more likely that the plumage of Type II is the result of some peculiarity in the gametic constitution of the bird.

Possibly an explanation of this peculiar behavior may be found in the following suggestions: In poultry breeding, what is known as the double-mating system is used to secure individuals which come nearest to the standard requirements. The term "double mating" means simply that two separate lines are used to secure the standard male and female respectively. The female from the standard male line and the male from the standard female line are wasters. In the last analysis, it means that to get a pair of show-room birds the females are bred from one strain, the males from another, each strain being carefully bred by itself. In Rouen ducks the breeder endeavors to produce a female with clean-cut concentric penciling of the type shown in plate VI, *o*. The male of the female line, though without penciling in the adult plumage, often has well-developed penciling in the juvenile or summer plumage, and, other things being equal, those males having the best penciling are chosen as breeders for standard females.

Under such selection it follows that the flock as a whole is held reasonably close to one end of the curve of variation. In the cross-breds the

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effects of this variation might be largely or completely lost and the character returned to the normal condition for the species. The feathers of the cross-bred female, while variable, are not penciled as a rule, but are splashed in various ways (plate VI, *m*). In the pure-bred stock, then, the constitution of the bird seems to be less variable, and even after the removal of the ovary tends strongly to continue its development in the same course that it had with the ovaries present. In other words, the constitution of the pure-bred female has been modified by selection in a given direction, so that it is in a measure independent of the internal secretion produced by the ovary. In the cross-bred, on the other hand, this modification has been lost for the most part and the female characters are dependent on the secretion of the ovary. Whether or not the explanation has any real basis in fact, it is evident that ovariotomy by itself is not always sufficient to transform a female into the replica of a male.

EFFECTS OF GONADECTOMY ON PARTICULAR PARTS OF THE BODY.

EFFECT ON PLUMAGE.

Of the various parts of the body affected by gonadectomy the most striking changes perhaps occur in the plumage of the female. The plumage of the male is altered comparatively little; some feathers grow somewhat longer, but otherwise they are the same as in the unaltered male. In contrast the plumage changes in the female after ovariotomy are extensive, both in respect to shape, size, color, and color pattern. Short feathers become long; straight feathers curved; feathers with broad rounded ends become narrow and pointed. A portion of the barbs become converted into bristles. The color changes are so numerous that only a few of them need be noted. Salmon feathers become black; stippled brown feathers become golden with a black central stripe, or black and brown penciled become gray and black vermiculated.

It is noteworthy that of all these changes none occurs in pairs, being promiscuous; this indicates that only two possibilities are available and that the action of the ovarian hormone determines which of the two possibilities develops.

EFFECT ON HEAD FURNISHINGS.

The Brown Leghorns offer especially good opportunities for determining the status of the capon's comb. It has been believed that his comb is that of the hen, and this is cited as an instance of the assumption of female characters by the castrated male. It requires only a cursory familiarity with the different races of fowl to observe that the size of the comb is an extremely variable character, although within certain rather large limits it is constant for each race. Thus, in certain

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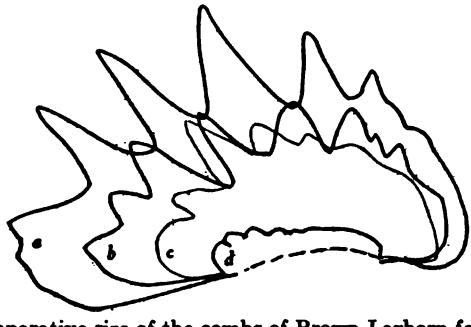
strains of Plymouth Rocks, the fully developed comb of the male is very much smaller than that of the Brown Leghorns, though the latter are only half the weight of the Plymouth Rocks. The female Minorca has a larger comb than that of the Plymouth Rock male, but, of course, the combs of the Minorca males are correspondingly larger. Moreover, in most instances the comb of the male has a proportionally larger blade than that of the female. A further difference is found in the texture of the comb, that of the female being finer than that of the male. Finally, in the female Leghorn and similar breeds the comb almost always lops to one side. This secondary sexual character is not universal among domestic fowl, but is most common in the Mediterranean races. Ordinarily, capons are derived from the low-combed races, a circumstance which has made it difficult to say that the capon's comb is not feminine. In the Leghorns, however, the capon's comb is practically undeveloped. Therefore, the only possible conclusion is that the capon's comb and wattles are infantile. They do not, of course, remain of the same size as that of the chick at the time of the operation. The base of the comb



Comparative size of the combs of Brown Leghorn fowls.

a, an adult male. *b* and *c*, two adult females. *d*, an adult capon. Drawing one-half natural size.

increases in length with the increase in size of the skull. The height of the comb also increases somewhat in absolute size, but not in proportion to the comb length. The comb of the Leghorn capon, however, is about the same size as that of some Plymouth Rock females. The comparative sizes of the combs of the normal Brown Leghorn, male and female, and of the capon are shown in the accompanying text-figure.

In the castrated females, the comb has developed in varying degrees, becoming very large and male-like in some, while in others it has remained comparatively small. As yet there is no clear evidence of the causes of this difference. Certainly it is not connected with the hypertrophy of the Wolffian body, for this has been found in every individual. The birds with large combs, as a rule, have been younger when castrated than those with small combs, but general conclusions can not be drawn from the few instances available.

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EFFECT ON SPURS.

There are contradictory statements in the literature regarding the effect of castration on the spurs of the male, some observers having even reported an absence of spurs in capons. All the capons reported in this paper have well-developed spurs, but it by no means follows that the observations to the contrary were incorrect, as in some normal cocks (Brahmas and similar races especially) the spurs are very slow in developing. One White Plymouth Rock male at 15 months had not developed a spur on one shank, while the spur on the other was very small. As far as my own experiments and observations go, the capon develops essentially the same amount of spur tissue as the cock. The spurs of the capon, however, develop somewhat differently. They become pointed soon after their eruption, and by the time they are half an inch in length they have the form of a perfect cone instead of the truncate cone of the normal male. Later they become indistinguishable from those of the adult male.

The normal female is usually without spurs, yet hens that in all other respects are perfectly normal, as far as outward appearances are concerned, sometimes develop spurs. In such instances the spurs may be of equal size on both shanks, symmetrical, and as long as those of the male; or they may be small, irregular in shape, and equal or unequal in size. In one individual observed, the left spur is a fine, long specimen, while the right is small and irregular in shape, projecting scarcely more than 5 mm. from the shank. Such hens are normal, at least as far as egg-production is concerned. The writer has had at various times several hens with well-developed spurs and has reared numerous chicks from them in the endeavor to produce a race of birds in which each sex might be spurred. As yet this result has not been secured, but that it is attainable is shown by the fact that some strains of Leghorns and Minorcas produce a large percentage of spurred female offspring. In one instance a Leghorn cock crossed on some Plymouth Rock hens gave a progeny of which the females were spurred in varying degrees. Thus, there is some indication that the origin of normal spurred hens is to be found in their genetic constitutions. The mere presence of spurs, then, is not necessarily to be taken as an indication of the assumption of a male character any more than the presence of horns in the female reindeer or domestic cattle is a similar indication of an abnormal ovary. If, however, the functions of the ovary as an organ of internal secretion is suspended, the spurs develop, and this development may continue even after the functions have been resumed. Well-developed spurs have been observed in all females castrated in which the male plumage also developed, while in many of those in which the assumption of male plumage was partial or temporary the spurs started to grow. Several times they continued to grow after the plumage reverted, and though they did not grow quite

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as long as those in which the removal of the ovary was complete, they were otherwise similar. The spurs became attached to the shank bone and had the same symmetry as those from completely castrated hens. Apparently, the dependence of the spurs upon the internal secretion is relatively slight, or, to look at the matter the other way, the inhibition exerted in the female upon the development of the spurs is so slight that once development starts the hormone is not always able to check it.

EFFECTS ON THE VOICE AND ASSOCIATED ORGANS.

Castrated ducks of both sexes, with the exceptions noted above, have undergone no change in voice. Each has retained the voice of the normal bird and each exercises its voice in a manner and to a degree quite the same as the uncastrated bird, except that some castrated females occasionally give voice to a sound similar to the drake's. Nor has any change been observed in the development of the syrinx in either sex.

In fowls the effects are more marked. Castrated individuals of each sex are disinclined to give voice to any sort of sound. Capons are capable of giving voice to all the sounds of which the cock is capable, but rarely do so, remaining (so far as ordinary experience goes) voiceless for long periods of time. Of course, it may happen that they use their voice more than noticed, but certainly to no such degree as that of the cocks nearby.

The castrated females have been equally quiet. I have never heard one crow or attempt to crow. One has occasionally been heard to cluck, making a sound that resembled the calling of the cock to the hens for a tid-bit. Another was induced to "cr-r-r-r-k" like a hen on one occasion. Aside from these instances, and a squawk when handled roughly, they remain voiceless.

EFFECT ON THE MOLT.

As far as my observations go, castration with one exception has not influenced the molt of the capon. A definite statement in regard to the molt of the poullard can not be made at present. In some instances a molt comparable to the summer molt of the ducks has occurred, with corresponding changes in plumage, as described for No. 4471. A comparable change, noted for No. 3840 and No. 2058 in 1915, has been described in detail elsewhere (Goodale, 1916). Other individuals, however, may not pass through such a molt, while the same individual may not show the molt each year. Thus No. 4471 exhibited the molt in 1914, but not in 1913 or 1915. No. 4290, though of the same age as No. 4471, did not pass through this molt in either of her two adult summers.

The castrated ducks, however, have behaved very differently. They molt several times each year and often without any definite relation to the normal molts of the adult. During the early period of their life, while they are growing the juvenile and adult coats of feathers, they molt at the same time that the normal birds do. The normal adult

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Rouen undergoes the following molts: Sometimes in early summer, usually in June and July, the actual date varying a great deal with different individuals, each sex molts, the new coat of the male forming the so-called summer plumage, while that of the female is not very different from that worn during the breeding plumage. Early in the fall each sex molts again, the male this time resuming his breeding plumage. The flights, however, are only molted once. Thus, there is an interval of 3 or 4 months during the summer when each sex is in a state of almost continuous molt in some part or other of the body. For the other 8 or 9 months the birds ordinarily retain the coat developed in the fall, *i. e.*, the breeding plumage. But the castrated individuals of each sex molt at irregular intervals throughout the year. The molt is extensive in that it includes nearly all the feathers except those of the wing. The new plumage is like the one that preceded it, except in the case of those females that have assumed the summer plumage of the male.

Castration of the drake has a remarkable influence on the summer molt. During the same period of the year that the normal drake is taking on the summer plumage, the castrated individuals molt, but do not assume the summer plumage. Instead, the new feathers are like the old. This is clear evidence that the testes control the characters of the summer coat. This coat imitates that of the female, but does not duplicate it, though feathers in certain regions of some males are indistinguishable from those of the female. Perhaps an explanation of this relation can be found in the following considerations: The summer plumage begins to develop when the breeding-season is at its height—*i. e.*, at the time of the greatest sexual activity—or at least soon after it has reached its climax, usually in June or early July. During this period the males are most active in treading the females and naturally the testes are at the period of greatest activity. The so-called breeding plumage, however, develops in early autumn, after the breeding season is over, when the males are least active and when the testes are in a state of comparative repose. The changes may or may not be connected with the greater production of spermatozoa at this season of the year, but may be dependent on some other physiological change in the testes. An attempt will be made to test this hypothesis by pulling feathers during the breeding season, some months ahead of the normal molt, on the assumption that the state of eclipse is due to changes in the testes resulting from their activity.[1]

Although it is perfectly clear that following castration the drake may not assume the summer plumage, it is not yet certain that complete castration in the sense of removal of both the spermatogenic portion and efferent ducts (epididymis) is necessary for this result.

[1]The experiment was tried in the spring of 1916, with results agreeing with the hypothesis proposed.

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EFFECT ON COLOR OF THE MANDIBLE.

The effect of castration on the color of the upper mandible does not correspond to that observed for plumage-color. No change has been noted in fowl and none is to be expected, since the color of the mandibles is the same in each sex of Leghorns. In Rouens the upper mandible of the male, both normal and castrated, is uniform greenish yellow, in the normal female dark greenish with a large central black area. In the cross-bred birds the mandibles may be yellow in each sex. In Gray Calls (Mallard in plumage color) the mandible of the male is greenish yellow with a blotch like that of the female. In the castrated female the central blotch remains, but the dark greenish color of the margin disappears, leaving these parts yellow. Castration, then, is without influence on the male's mandible color, but removal of the ovaries results in the disappearance of certain pigments from the mandible of the female, regardless of the age at which the operation is performed.

The newly hatched ducklings are alike in the color of the mandible, which is almost black. During ontogeny that of the male lightens up uniformly until the adult color is reached; that of the female, however, lightens in certain regions only, corresponding to the pattern described. In one lot of ducklings a month old the differences in mandible color were already apparent. Probably it will be necessary in operating to anticipate such changes if a modification of the mandible color is to be secured, but thus far attempts to ovariotomize ducklings a week or two of age have failed. We are unable, consequently, to determine the exact relationship between the ovary and the blotch in the female's mandible. It is hazardous to assume, from analogy with other characters, that the female mandible color is really dependent on the ovary, but that its pigments have been deposited in an unchangeable state, comparable with that in a fully formed feather. Instead it is possible that it is a unit character inherited according to some definite but unknown scheme. In Gray Call ducks, as pointed out, the male has the central blotch as well as the female. The male Rouen, exceptionally, may have the ridge of the mandible darker than the rest. Since the "Standard of Perfection" calls for the mandible color described above, it becomes more probable that the blotch represents a separate unit character.

EFFECT ON SIZE.

It has long been known that the male mammal and bird, when castrated young enough, grow larger than intact individuals. This is due in part to the continued growth of the epiphyses of the long bones, though at the same time there is a general increase in size. The present set of experiments has not been of sufficient extent, nor has the stock been sufficiently homogeneous in respect to weight, to give average results of any value whatsoever. That is, the variation among normals is so great that a comparison with the few castrated individuals might be

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misleading. Nevertheless, some general statements may be made. While the Brown Leghorn capons are obviously somewhat larger than the normal male, such a condition is not so obvious in any of the castrated drakes, although the weights indicate some increase in size.

The castrated ducks approximate the size of the normal female. The castrated pullets, too, remain about the same size as normal pullets, although they seem relatively small. The apparent lack of size is due to the fact that the legs remain small, like those of the hen, while the plumage develops like that of the cock, thus producing a small-bodied, short-legged bird quite different from the cock or capon with large frame. All that can be said of the size relations at present is that the body-size of the castrated pullet does not exceed that of her normal sister. The shanks, likewise, though spurred, are of the same size as those of the normal female.

EFFECT ON BEHAVIOR.

Completely castrated individuals of all kinds are on the whole negative in behavior as compared with normal adults. The behavior of castrates corresponds rather closely to that of young birds shortly before they become mature. The birds eat, drink, and move about rather quietly. The capons do not ordinarily crow or pay any particular attention to the hen. They are not pugnacious, and if attacked will not often fight. The poullards never visit the nests, never "sing" or cackle, show none of the normal female sexual reactions, and few or none of the male's. The castrated ducks are neither more nor less noisy than their mates, but sexual behavior is wanting. Normal drakes sometimes attempt to tread castrated females (Type I as well as Type II) that are kept in the same pen. The duck, however, attempts to escape, so that the male gets little satisfaction. Evidently the color loses any value it may have had as a recognition mark. On the other hand, castrated females introduced into a strange pen have been treated at first as a strange male. It is clear, too, from the behavior of hens when a poullard is introduced into a pen which contains no male that they regard the poullard as a male. The poullard, however, does not behave as a male, but is rather indifferent, though in one test the bird was extremely pugnacious and attacked every hen that approached.

EFFECT ON ACCESSORY ORGANS OF REPRODUCTION.

Most of the birds operated on are still alive, so that general statements only can be made regarding these organs. Usually the vas deferens in both castrated drakes and capons can not be found unless there has been a considerable regeneration of spermatogenic tissue; but occasionally it remains visible as a thin strand of tissue with few or no convolutions. The papillæ of the capon also have not been found, but as these are very small in the cock, such a result is not surprising. In

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drakes, the penis has always been found, sometimes rather smaller and more flaccid than usual, but otherwise essentially the same as that of an intact drake.

In the castrated female the oviduct has always been found. It is larger than that of the young chick, corresponding in its dimensions to the increased size of the bird, but otherwise is entirely infantile. In this respect it is like the comb of the capon. The increase in absolute size of oviduct is mainly in length, with a slight increase in width, quite like that of a young pullet prior to the enlargement of the oviduct in anticipation of laying.

EFFECT ON THE BURSA FABRICII.

This is not a secondary sexual character, but like the thymus is essentially an organ of the young and undergoes involution at or near maturity. As slight attention was paid to it until its persistence was noticed in two completely castrated drakes, little can be said of it now. In incompletely castrated males it can not be found. Future observations may show that some intimate relation exists between it and the primary organs of reproduction.

OCCURRENCE OF CHARACTERS OF ONE SEX IN INDIVIDUALS OF THE OPPOSITE SEX THAT ARE OTHERWISE NORMAL.

MALE CHARACTERS IN THE OTHERWISE NORMAL FEMALE.

The most conspicuous of these characters are spurs which occur in some females that otherwise are apparently normal. In plate VII, *B*, are shown the shanks of a White Leghorn hen now 8 years old. The spurs, while somewhat more slender than those of a cock, *i. e.*, in proportion to her shanks, are otherwise quite as male-like as could be wished. In other respects the bird is entirely female in character, even her head furnishings being feminine. She has laid well and her eggs have hatched well. This bird was about 2 years old when the spurs were first noticed. At that time they were as well developed as in cocks of the same age. Another hen, No. 1055, related to the first, also has a fine pair of spurs. They appeared when the bird was 6 months of age as blunt stubs exactly like those of a cockerel, and by the time she was a year old they had enlarged and become as pointed as those of any male of the same age. Both these birds have been bred from, and a hundred or more chicks hatched, but because of certain circumstances few of the pullets have been kept sufficiently long to develop spurs and these appeared in only one of the few kept. But the fact that spurred females appear in large numbers in some strains indicates that, at bottom, the spurs in the uncastrated female depend upon some hereditary factor or combination of factors.

The comb and wattles of some females are often very large, giving the bird a masculine appearance. In Leghorns and other large-combed breeds the large combs in the female are not considered masculine,

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even when the lop is absent. If, however, a pullet with an erect comb of similar size appears in a flock of Plymouth Rocks, she looks masculine. However, the proportions of the comb are usually unlike those of a male, and it also seems probable that if the bird had been a male the comb would have been several times the size it actually attained. In other words, such birds are simply large-combed but not masculine-combed females.

In Mediterranean breeds the comb of the male is erect, that of the female lops. Females, however, frequently occur with erect combs, which, however, are of female size and proportions. In some males there is a tendency for the comb to lop, particularly when young, though it never does so in quite the same fashion as it lops in the female. While the comb of the female never lops after complete castration, the comb of the young capon lops sometimes, like that of the young male. There is no reason, however, to believe that the lop of the adult female and that of the young male are due to the same causes. The lop observed in the comb of young males usually (but not always) appears due to lack of stamina or to some environmental causes, such as an injury.

The exposed surface of the secondaries constitutes the wing bay. In the female of those races where there is a sex differential coloration of the body this area is stippled. In Brown Leghorns the stippling is light brown on a dark-brown ground-color. In the male it is a solid color—a uniform red in the Leghorns. While the stippled condition may be transitory in the young male, it has not been observed in the adult, either normal or castrated. In some cross-bred females belonging to the writer, the wing bay of the females is a solid color and its feathers would readily pass for a male's feathers from that region. A condition of this region, intermediate between the male and the female, often appears in Brown Leghorn females, and associated with it is a condition known as "brick" by the fanciers. The brick is a reddish color of the wing-bow region, exactly that region which in the male is red. Its appearance strongly suggests a heterozygous condition, but no breeding tests have been carried out.

In ducks, so far as I know, the only male character that appears in otherwise normal females is the neck ring, though it is reported that normal females sometimes develop the curled tail feathers of the male. In one instance the neck ring appeared when the duck (a Rouen with typical female plumage) was less than a year old, but it is not known whether the duck laid or not. In hybrid females there are several types of neck rings, among them one like that of the male Rouen or Mallard. On the other hand, some hybrid males show no trace of a neck ring. One or two females of this race lacking neck-rings have been castrated and they, too, have not developed any ring, though otherwise they have been among the most perfectly male-plumaged individuals.

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On the other hand, there are male characters which never seem to occur in the *unaltered* female, such as male saddle feathers, sickle feathers, black breast in Brown Leghorns (though *self-colored* brown breasts occur, the individual feathers of which are stippled), while in ducks vermiculated feathers, body pattern, etc., syrinx, bill color, etc., have not been observed in the normal female. Brandt, however, cites instances of fertile cock-feathered females. In general, then, it seems highly probable that some intimate relation exists between the germinal constitution of the female and the appearance in the normal individual of certain characters usually found only in the male. Also, it is interesting to note that these characters appear in the ducks of Type II, described above. Obviously, there is some close relationship between the gametic constitution of an individual and the internal secretion of the germ glands.

FEMALE CHARACTERS IN THE OTHERWISE NORMAL MALE.

Instances of the occurrence of female characters in males, strictly comparable to those just described for the female, are uncommon or wholly lacking. It has already been shown that the only character of this sort among capons is the brooding instinct. One reason for the non-occurrence of such cases is found in the few characters that it is impossible to confuse with juvenile conditions. Brandt records only two or three doubtful instances of this sort among a large number where females exhibited male characters. On the other hand, when female characters occur in the male they either form part of a normal cycle, such as the winter plumage of the bobolink, or the laterals in the summer plumage of the drake, or they are breed characters, such as hen feathering, discussed below. We may, perhaps, distinguish two categories of secondary sexual characters, viz, those absolutely dependent on the internal secretion of the gonad and those partially, at least, independent, and if this be true then those male characters occurring sporadically in females otherwise normal are in essentially the same class as the occurrence of female characters in the otherwise normal male.

HEN-FEATHERED MALES.

These birds are of great interest from several standpoints. The classical example is that of the Seabright bantams, yet it is stated in the history of this breed that the hen-feathering originated outside. Doubtless, hen-feathered males have long existed. They frequently occur as "sports" among Hamburgs, while among Campines two types of males are recognized, the English or hen-feathered and Belgian or normal type. These hen-feathered birds are fertile, though the statement has been made for Seabrights that those which are most strongly hen-feathered are inclined to be sterile. Possibly the reason is to be found in an inherited condition of sterility. Hen-feathered males have their other male characters well developed. However, the

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writer has never seen a hen-feathered male in a race where the females were of the Brown Leghorn or Dark Brahma type of color. Whether or not the males of such a race would take the female's color on becoming hen-feathered is unknown.[1] In Hamburgs, Seabrights, and Campines the normal male is colored like the female in some parts of of the body at least, a color which is often very like that of the juvenile male, so that it is impossible to ascertain whether or not the coloration of hen-feathered males is female or not. In regard to the shape of the feathers, a more definite statement can be made. The shape of the feathers of the hen-feathered male is exactly like those of the juvenile coat of the male, but as these are also the same shape as those of the female, they furnish us no proof of the assumptiom of a female character by the male. In addition to normal male-feathered cocks in these races, I have seen a third type, in Campines, in which part of the feathers of the regions under discussion are male, while the rest are juvenile (or female). Such birds always looked ragged and are very suggestive of the condition of young males at the molt between the juvenile and male plumage. According to some experiments that have been reported by various observers, it is certain that the hen-feathered condition is a definitely inheritable character.

Since the castrated male in normal races develops normal plumage, and since the hen-feathered character is undoubtedly an inheritable character, it seems better to refer the condition to a factor which alters the form of plumage. Perhaps it is an inhibitor. Naturally, since the female already has the same form of feathers, she will not exhibit any modifications. If this had been the normal feathering of *Gallus bankivus*, as it is in the turkey or duck, the appearance of a new form of feather in the male alone would constitute a new secondary sexual character. The assumed primitive male, however, would not be hen-feathered. Looking at it from this standpoint, it is evident that we must give due regard to the part played by inheritance. At present, I believe we are unable to point to any female-like character in males that is not also juvenile.[2]

INHERITANCE OF SECONDARY SEXUAL CHARACTERS.

Disregarding for the moment Type II, it is apparent that the inherited base for the secondary sexual characters in each sex is the same—that is, the characters in each sex, except for the secretion of the ovary, would be alike. In other words, there is no problem of the mode of inheritance of secondary sexual characters in birds such as there is in insects, where these characters are independent of the gonads. The secondary sexual characters are inherited in exactly the same fashion

[1]Morgan, 1915, has found that such males take on the female's color.

[2]Since this section was written, Morgan, 1915, has shown that the hen-feathered condition in the male is due to an internal secretion of the testes.

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as many other characters which are exactly alike in each sex. The sole difference lies in the ovary. Moreover, the genetic factors that are transmitted, if expressed in terms of their somatic results in the absence of the ovary, are the male characters. In this connection it is important to note that the castrated females have always taken the characters of the male of the race to which they belong. This has been particularly noticeable among the cross-bred ducks, where there are several distinct types. In crosses, then, each sex transmits the same set of genes, while the resulting characters are modified by the ovary into the proper female somatic characters. Unfortunately, however, such a simple solution of the breeding problem is not of universal applicability. The presence of the Type II female, together with certain characters, such as mandible color, stands in the way. Here recourse was made to the genetic constitution of the bird to explain their appearance. Attractive as the ovarian-secretion explanation may be, it does not entirely do away with the need for an explanation of the inheritance of secondary sexual characters.

The mode of inheritance of the internal secretion is a different thing from the inheritance of secondary sexual characters as such. Obviously it is closely connected (coupled or linked, if you like) with the inheritance of sex itself; so closely indeed that the two can not be separated by any means now available. We must for the present treat it as if it were "femaleness," unless the following hypothesis seems more desirable. The genes for the secretion may be considered to be inherited independently of the sex genes, but just as the Müllerian duct disappears in the male, so the mechanism for the production of the secretion may also disappear in this sex. Such a scheme does away with the use of sex-linked inheritance in this connection.

IS THE FEMALE BIRD A SUPPRESSED HERMAPHRODITE?

A true hermaphrodite possesses both ovary and testes with their respective products, ova and spermatozoa. There is no direct evidence, then, that the female fowl is a potential true hermaphrodite, since spermatozoa have not yet been observed in castrated females. However, the presence of certain accessory organs of reproduction following ovariotomy points strongly in this direction. The anlagen of both vas deferens and oviduct occur in each sex, and so each sex might be considered to be a potential hermaphrodite. It is certain, moreover, that the Müllerian duct completely disappears in the male, but apparently the Wolffian duct and body may not always degenerate in the female. There is good evidence from *breeding* that the female is a sex heterozygote, though the *cytological* evidence in this respect is negative, resting on the failure of Boring's and Pearl's work to substantiate Guyer's report of an accessory chromosone (sex heterozygotism) *in the male*. Though in many instances there is indisputable evidence that sex is determined at the moment of fertilization, there is other evidence

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that sex, in the sense of the separation of male from female sex cells, may be determined after fertilization; for example, in normal hermaphrodites, such as *Helix*, *Lumbricus*, etc., and the many instances among plants. Among the latter, many regions that normally produce macro- or micro-spores may, under a suitable stimulus produce the other kind. Neither the assumption of male plumage by the female nor the development of the accessory reproductive organs need be considered evidence that the female is a suppressed hermaphrodite, because the secretion of the ovary clearly controls their development. On the other hand, it is clearly proven that the female is a suppressed *pseudo*-hermaphrodite.

If there is any basis in fact that the normal female is a suppressed hermaphrodite, then, since there is no reason to believe that the male is an hermaphrodite, those avian hermaphrodites that occur in nature must arise through a failure of the mechanism for the suppression of the male in normal females.

Unless and until ovariotomy should be found to result in actually converting a female into a male with spermatozoa, thus demonstrating that the female is a suppressed hermaphrodite, the effects of castration on the secondary sexual characters can not be said to have a bearing on the problems of sex determination. They demonstrate rather the existence of a mechanism for the control of the secondary sexual characters that is so closely associated with certain parts of the mechanism for the determination of sex that the two go together, except, perhaps, in races of the Seabright type.[1] The association, however, throws no new light on the mechanism by which sex is determined, unless we wish to extend the idea of internal secretions by assuming that all individuals are hermaphroditic and that at some period after fertilization a mechanism comes into operation that partially or wholly suppresses the opposite sex. It is conceivable that the secretions of certain cells in the embryo may determine which class of primitive ova develops. The result would be the same, of course, as if the usual sex scheme is followed, with this difference, that the determining mechanism is not in itself sex. Such a scheme would account for the appearance of the Müllerian and Wolffian ducts and associated parts in all embryos.

THE RELATION BETWEEN BREEDING AND GONADECTOMY.

The results obtained from gonadectomy have considerable bearing of a practical nature on inheritance studies in poultry. We need no longer erect separate categories for characters that appear in one sex only, but may classify a given character in the female with the corresponding character in the male, even though the two characters actually appear very unlike. These remarks apply naturally only to those characters that are actually modified by the internal secretion of the ovary, while due regard must be paid to the exceptions noted where the castrated female does not develop a normal male plumage.

[1]See note 2 page 46.

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DARWIN'S AND WALLACE'S THEORIES OF THE ORIGIN OF SECONDARY SEXUAL CHARACTERS.

Both of these theories assume that the difference between the sexes has arisen through selection—natural selection according to Wallace, sexual selection according to Darwin. Birds, in particular, have furnished illustrations in support of each theory. Natural selection is assumed to have operated through the survival of those females that were more protectively colored than their mates. The theory of sexual selection assumes, on the other hand, that the males acquired their present-day colors in response to selection on the part of the females, which chose the more highly colored males. According to Darwin's theory the start was made from a dull-colored monomorphic species, an assumption that is not in accord with the nature of the female as shown by castration, since the brilliant male colors are merely suppressed in her. The only possible effect of selection, then, would be the uncovering of a condition already present. But, by hypothesis, this condition did not pre-exist.

Wallace's theory, starting also with a probably dull-colored monomorphic species, is in partial agreement with the results of castration. It must be modified by assuming that natural selection acted indirectly through the development of an internal secretion of the ovary *pari passu* with increased brilliancy of the male rather than on the characters themselves. Since, however, the female possesses the same potentialities as the male, the start may have been from a highly colored form rather than the reverse.

NATURE AND MODE OF THE OVARIAN SECRETION.

The adjustment of the ovarian secretion to the characters it modifies is very close, as shown by the fact that the male characters produced in a given female are like those of the corresponding male. This must mean that the large element in determining the result is the heredity basis and not the secretions. From this we may conclude that the secretion on the whole is relatively simple and probably of uniform nature. If the secretion were composed of many substances, one to produce each effect involved, such as the change from a vermiculated feather to penciled, from a gray and white to a black and brown, the resulting complexity would be so great that one would not anticipate any such close coordination as actually results. For purposes of illustration we may assume that the ovarian secretion is simple, producing its effect by oxidation or some other simple process. The sort of result produced by oxidation, of course, depends upon the substance that is oxidized.

From another standpoint, the question may be raised as to whether the secretion should be considered as a modifier or an inhibitor. If it be assumed that it is a modifier, only one genetic basis need be assumed

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for each sex, *i. e.*, the genetic basis that is responsible for the male secondary sexual characters. The modifier changes over the male characters into the female characters. On the other hand, an inhibition requires the assumption of two genetic bases (factors or group of factors), one responsible for the male secondary sexual characters, the other for the female. In the absence of the ovarian secretion, the male characters appear. If the secretion be present, it inhibits the male characters and allows the female characters to appear. In some respects it is simpler to assume that the internal secretion actually changes over the male characters into female because only one genetic basis need be assumed. The back, wing-bow, and saddle feathers in particular fit in with such an assumption. In the male the barbs lack the barbules on their distal half, *i. e.*, are bristle-like, though they are present in the female. In Leghorn males the juvenile feathers of this region have barbules, but they disappear on the adult feathers, though in other races individuals often occur which lack the juvenile coat in this region, growing adult feathers directly from the down follicles. Something must prevent the development of the barbules in the adult; therefore, if the ovarian secretion is an inhibitor merely, we have an inhibition of an inhibition. The inhibition of barbule development in the male must be germinal, for it is certainly not testicular, since after orchidotomy the barbules do not develop.

In the last analysis the effect of the ovarian secretion comes down to its effect on the cells, either the cytoplasm or nucleus, but if the control of the direction of developments lies in the chromosomes, then the influence of this secretion must be exerted upon these through the intermediation of the cell protoplasm.

In the formation of the various colors it is possible to conceive of a mechanism whereby the internal secretions combining with an enzyme, or possibly acting as such, are able to change the color. Such an explanation, however, seems insufficient to account for the arrangement of cells in the feather, the number produced, and whether or not they have processes (hamulæ).

We may, however, conceive that the presence of the ovarian secretion in the body fluids surrounding the cells influences their development in much the same way that modifications of characteristics are induced in organisms by the environment. The secretions, indeed, must be considered part of the environment of each cell. The cells, however, respond only when in a growing, or, at least, active condition. Feathers, for example, change color only at a molt, so that a bird might be castrated and never change color for nearly a year. In this respect the secretion is like all other environmental factors.

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RELATION BETWEEN THE GONADS AND THE SECONDARY SEXUAL CHARACTERS IN OTHER GROUPS.

The influence exerted by the gonads on the secondary sexual characters varies from group to group. In insects, the secondary sexual characters are independent of the gonads. In certain crustaceans conditions are the reverse of those found in birds. In mammals, removal of the testes produces an effect very similar to that on the male bird. The female, however, undergoes very little change in her secondary sexual characters. Steinach, however, has shown that by transplanting ovaries into the castrated male—rat or guinea-pig—he becomes feminized. Bresca found in *Triton* that the crest of the tail did not develop after castration, while Nussbaum found for the frog that the thumb pads failed to develop, though Smith secured results opposed to Nussbaum's.

On the whole, the relation between the gonads and the secondary sexual characters appears to be specific and not general. Although more striking, their relation is essentially of the same order as other morphogenetic secretions, such as that of the thyroid. Indeed, the morphogenetic activity of the gonads is by no means confined to the secondary sexual characters, but produces other well-known effects.

SUMMARY.

1. If the ovary of a domestic bird be removed completely, many of the secondary sexual characters of the male appear. Some individuals become nearly complete replicas of the male, others imperfect imitations of the male.

2. If the testes be removed, the majority of the secondary sexual characters of the male develop, though a few may remain in an infantile condition.

3. Castrated drakes lose the power of developing the summer plumage.

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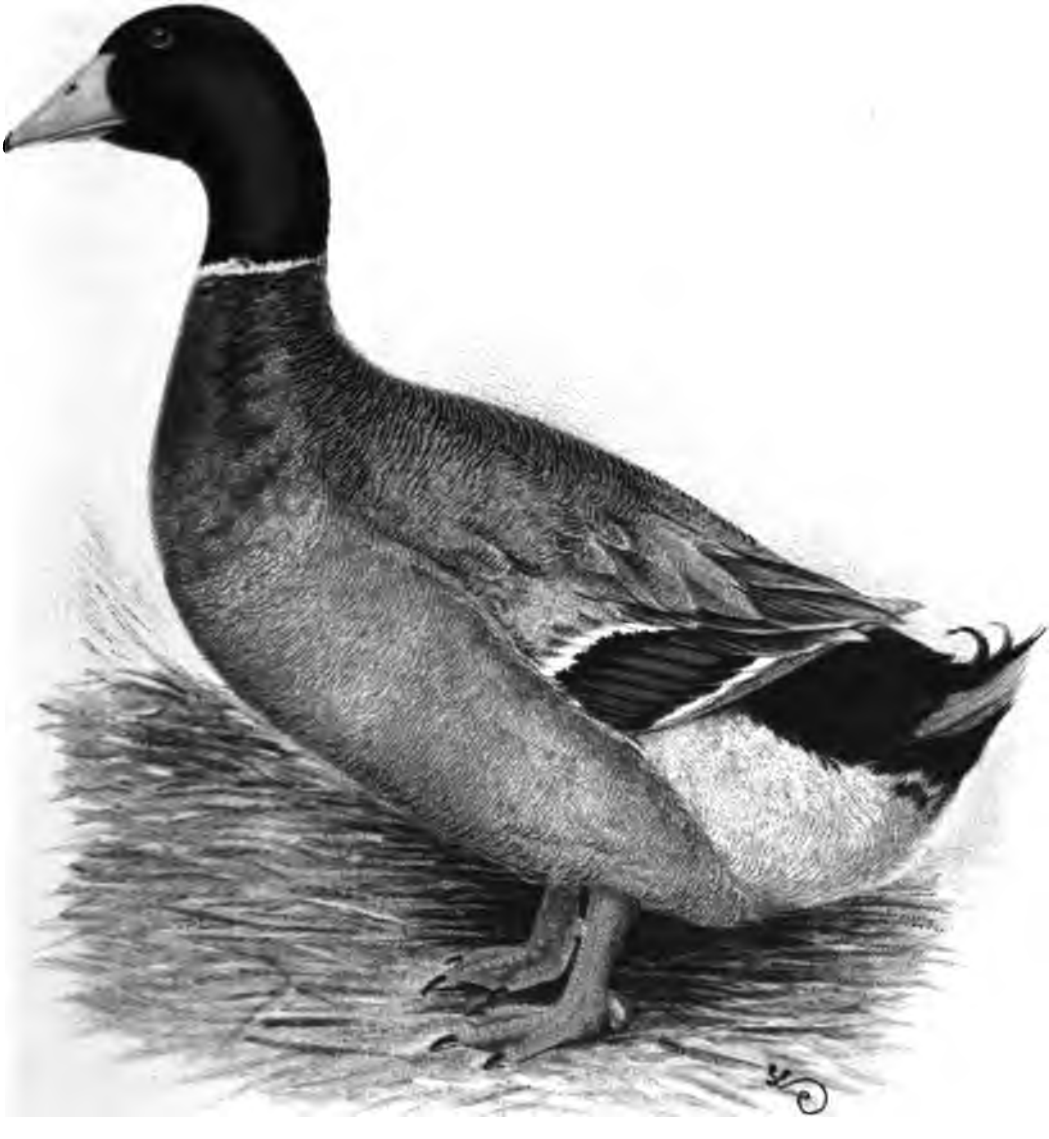

NORMAL ROUEN DRAKE.

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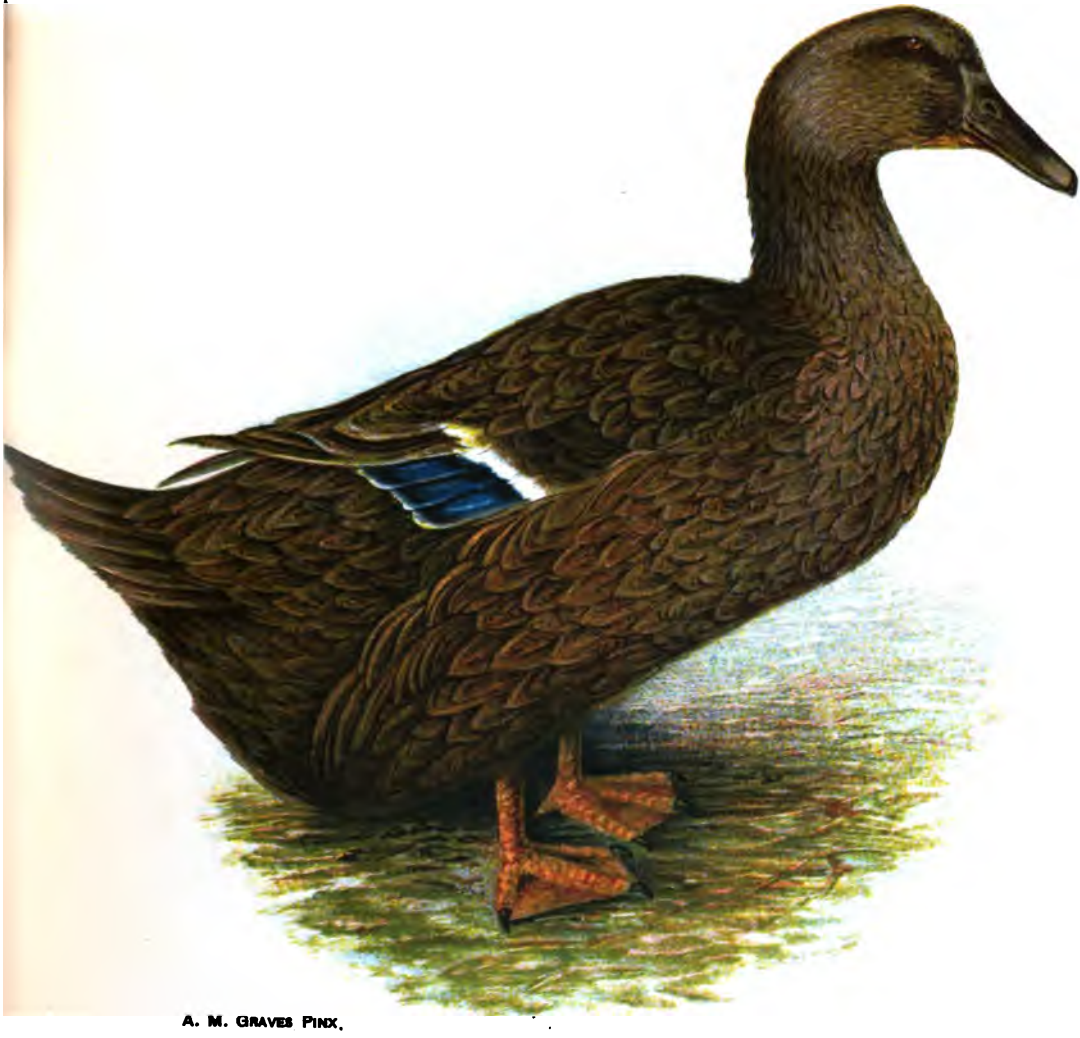

A. M. GRAVES PINX.

NORMAL ROUEN DUCK.

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A. M. GRAVES PINX.

AN OVARIOTOMIZED DUCK, NO. 169, TYPE I.

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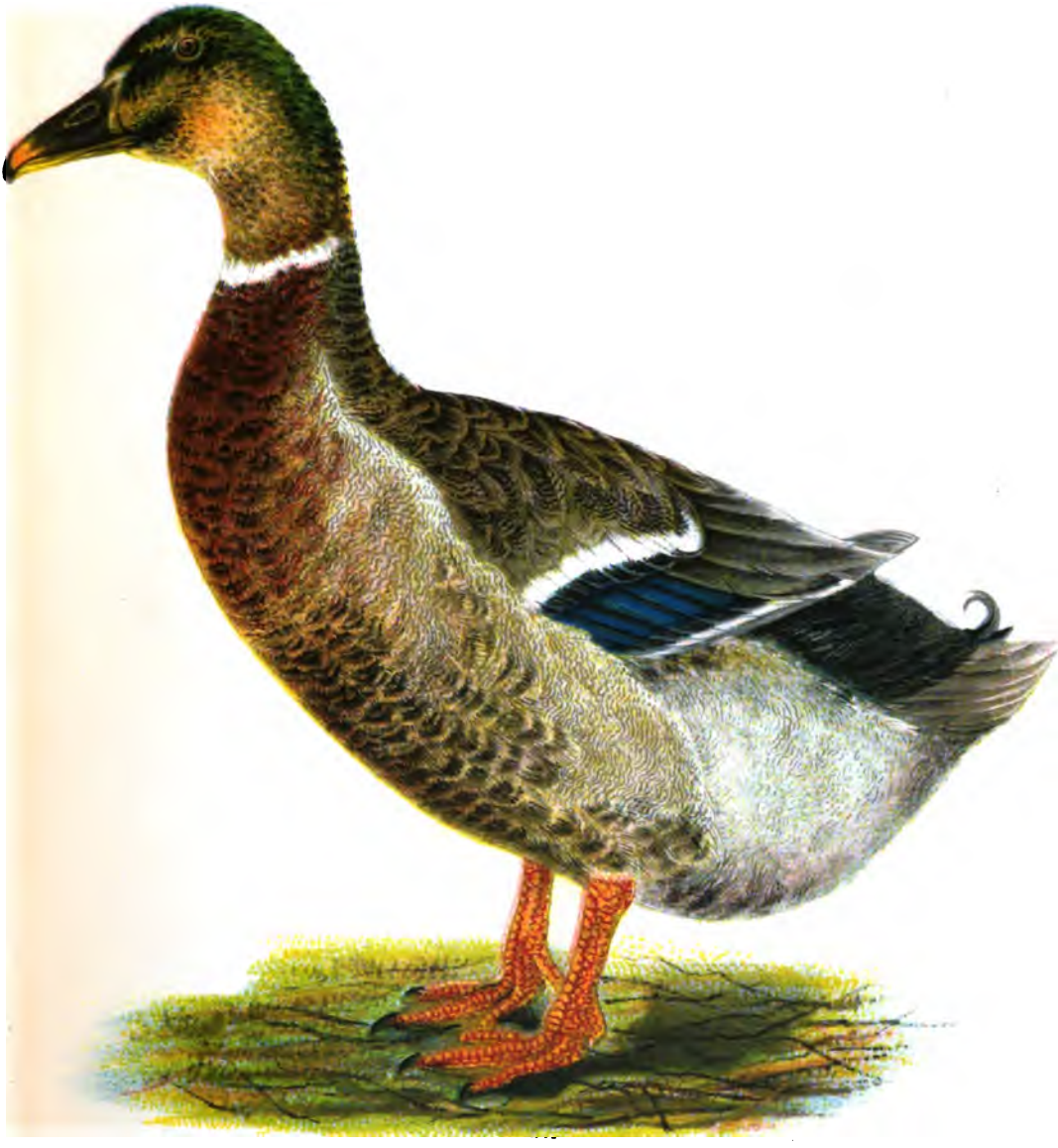

K. MORITA, PINX.

AN OVARIOTOMIZED DUCK, NO. 24, TYPE II.

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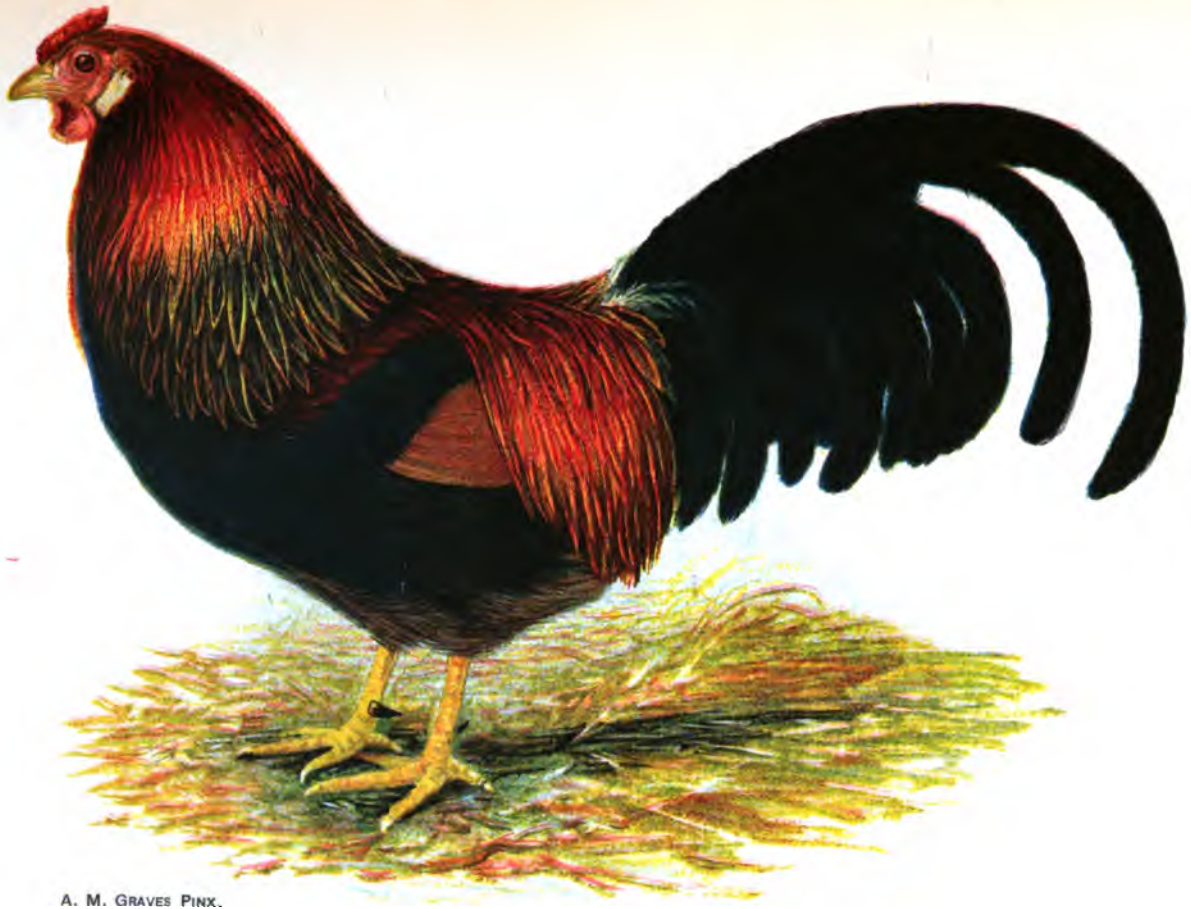

A. M. GRAVES PINX.

OVARIOTOMIZED PULLET.

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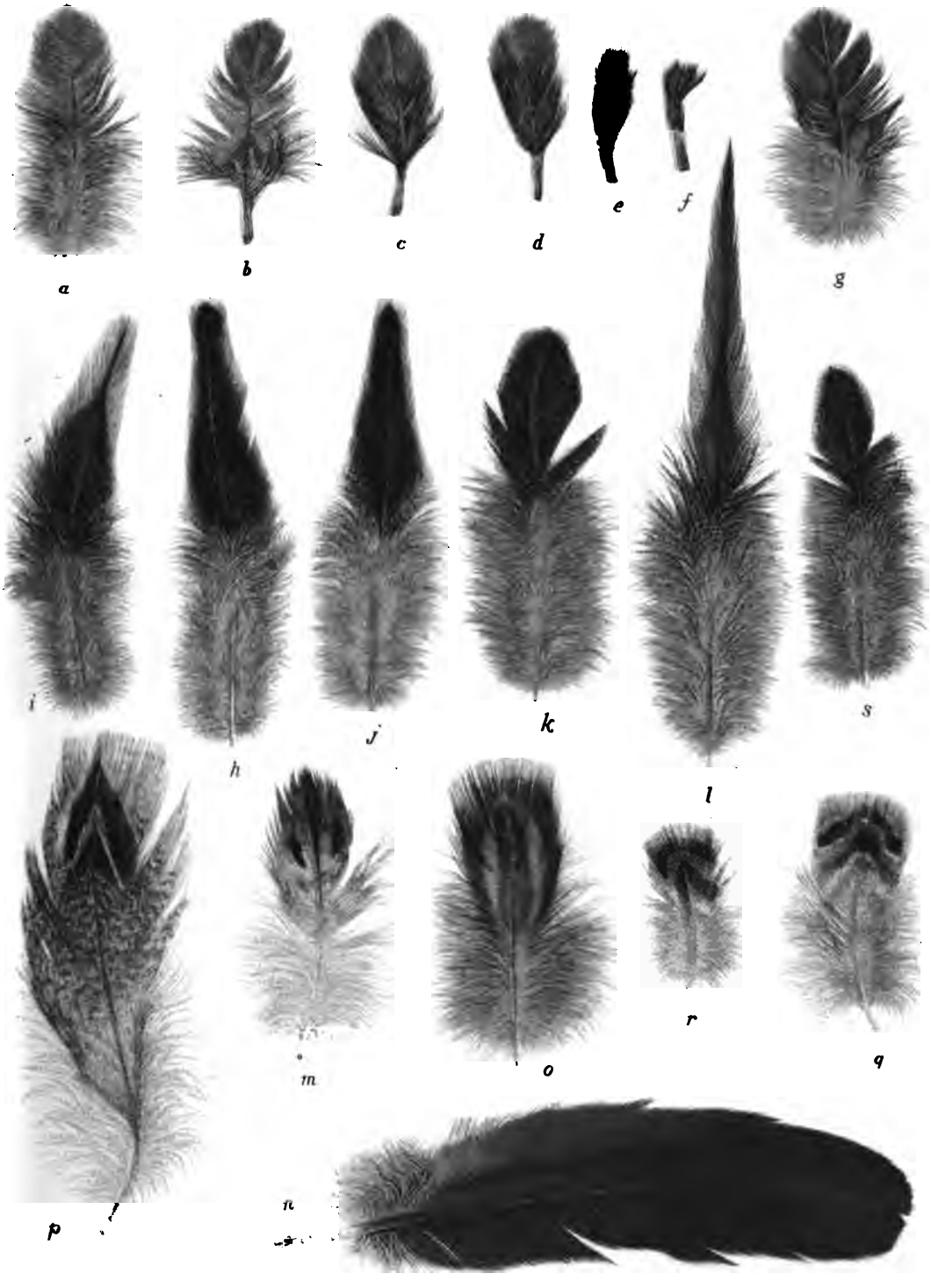

THE EFFECT OF OVARIOTOMY ON PARTLY-DEVELOPED FEATHERS.

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A

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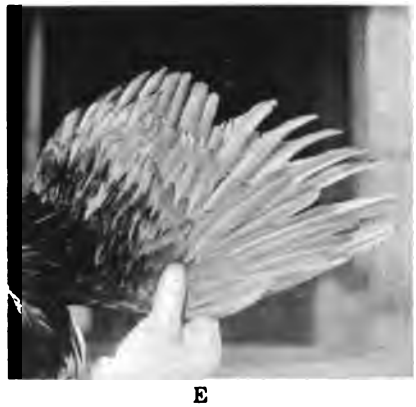
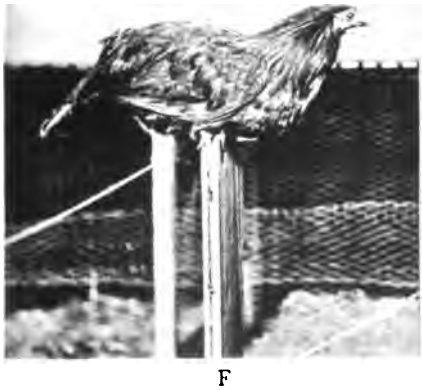


E



F

G

A. Head of capon, showing infantile comb and wattles.

B. Shanks of White Leghorn hen described on page 43, showing long spurs.

C. Reproductive system of No. 1196; *rd*, right body with duct, *rd*, leading therefrom; *lb*, left body and duct, *ld; o*, oviduct (not clearly shown in the photograph); *int*, intestine.

D. Two young ducks (No. 169 front and No. 171 rear), showing condition soon after castration.

E. Wing of capon showing the hypertrophied primary coverts.

F. Partially ovariotomized female, showing a few male feathers among the female feathers. The male feathers visible in the illustration are the hackle feathers and the black feathers in the wing.

G. Capon with a brood of chicks.

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